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THE GEOGRAPHICAL DISTRIBUTION OF FRESHWATER  
DECAPODS AND ITS BEARING UPON  
ANCIENT GEOGRAPHY.

BY DR. A. E. ORTMANN.



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INTRODUCTION.

During the last decennium Zoogeography has developed in a very peculiar direction, which, in a large part, is directly opposite to the methods introduced by Wallace. The professed aim of the latter was the creation of a zoogeographical division of the earth's surface into regions, realms and the like, the purpose of which was the subordination of the facts of animal distribution under a fixed scheme; and since it was self-evident from the beginning that the distribution of animals ought to express the physical conditions of the earth's surface, it was assumed that the proposed zoogeographical divisions correspond to the chief features of the distribution of the conditions of life.

Soon, however, it was discovered that it is impossible to give a division of the earth's surface that could claim general recognition. It is true that each of the proposed schemes was actually supported by more or less numerous instances of distribution, and that in many cases the physical factors influencing and explaining these divisions were easily understood; but there was always alongside of the supposed normal conditions a number of exceptional cases, where the actual distribution of certain animals or animal groups was directly the opposite. One of the chief causes of this fact has already been recognized and carefully studied by Wallace. It is

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the difference of the means of dispersal of the various groups of animals. On account of these anomalies Wallace constructed his regions chiefly for Mammals and Birds, excluding all the rest of the animal kingdom.<sup>1</sup>

This method, however, can never be satisfactory. It amounts to nothing but the creation of an arbitrary scheme which may correspond to some of the facts; but if there are any other facts that do not fit into it—as very often happens—they are simply thrown out and neglected.

But this is not all. Even the restriction of Wallace's regions to a single group of animals proved insufficient to cover all cases within this group. This is true also of all other schemes that have been proposed by other writers for the same or other smaller groups. In every single instance there were exceptions to the rule, and for some time it seemed difficult or even impossible to deal with these apparent anomalies; in fact, none of the proposed divisions into regions can be applied to all cases, even within smaller groups.

The correct understanding of this fact, that a large number of animals does not submit to any of the proposed schemes that profess to comply with the present distribution of the condition of life, was made possible by the consideration that the actual distribution of any animal must have originated in the past. Although there are some animals the history of which does not go very far back, in a geological sense, there are others which do, and, generally speaking, we may say that the farther back we go in geological history the more different were the conditions of life from what they are now, and the present distribution of the respective forms must necessarily appear the more strange and anomalous. Wallace, indeed, tried to remove this difficulty in a very peculiar way. He simply propounded his principle of the permanency of the continents, which means to say that the present distribution of land and water (and in general of the physical conditions of life) did not change materially during the earth's history, and that the external features of the earth's surface have remained practically identical from time immemorial up to the present. That this principle is without

<sup>1</sup> This exclusive restriction to the higher forms of life (Mammals, Birds) is a principle of Wallace and has been expressly maintained by him as late as in 1894 (see *Nature*, Vol. xlix, 1894, p. 610).

proper foundation has now been recognized and the opposite opinion begins to prevail, that abnormal conditions of distribution are due to just such changes of the physical conditions during a geological past, and that cases of this kind may often enable us to draw conclusions as to the reconstruction of the old conditions. We may safely assume that the character of the physical conditions of the earth's surface has changed continuously and variously in the past and that we possess among living animals many forms which express in their present distribution not only the Tertiary state, but which may also represent Mesozoic or even Palæozoic conditions. Thus it is evident that investigation of the present distribution cannot be used as the starting point for the construction of any scheme. This has been done, however, not only by Wallace—who entirely disregarded the above fact—but also by others, who paid due attention to it. Indeed Osborn<sup>1</sup> has pronounced it the purpose of Zoogeography to unite past and present distribution into one scheme, and the same idea has led Jacobi<sup>2</sup> to attempt practically this union.

But if we study the most prominent differences between past and present we see that they are chiefly found in the different distribution of land and water, and that frequently in past times land connections existed between parts which are now separated, or *vice versa*; and thus it is self-evident that the solution of Osborn's problem is simply impossible, since there is no way to express separation and connection of the identical parts in one and the same scheme.<sup>3</sup>

We consequently arrive at the following three conclusions:

1. *Any division of the earth's surface into zoogeographical regions which starts exclusively from the present distribution of animals, without considering its origin, must be unsatisfactory, since always only certain cases can be taken in while others remain outside of this scheme.*

2. *Considering the geological development of the distribution of*

<sup>1</sup> H. F. Osborn, "The Geological and Faunal Relation of Europe and America During the Tertiary Period, etc.," in *Ann. N. Y. Acad. Sci.*, Vol. xiii, 1900, p. 48, and in *Science*, April 13, 1900, p. 563.

<sup>2</sup> A. Jacobi, "Lage und Form biogeographischer Gebiete" (*Zeitschr. Ges. fuer Erdkunde*, Berlin, Vol. xxxv, 1900).

<sup>3</sup> This, of course, does not dispose entirely of Osborn's problem. On the contrary, it remains "the" problem of Zoogeography, only we have to change its formal expression and to say that the *historical union* of past and present distribution is the purpose of zoogeographical study.



*animals, we must pronounce it impossible to create any scheme whatever that covers all cases.*

3. *Under these circumstances it is incorrect to regard the creation of a scheme of animal distribution as an important feature or purpose of zoogeographical research.*

Thus we are justified in saying that zoogeographical study, as introduced by Wallace, is not directed in the proper channels, and we are confronted with the question, If the creation of regions of animal distribution is not a matter of first importance, which is the vital point in this branch of research?

This question has been practically answered by many writers. I name the following: G. Pfeffer, E. von Ihering, H. A. Pilsbry, R. F. Scharff, C. Hedley, W. Kobelt, H. F. Osborn, A. Jacobi (besides others), and these we may take as representatives of the modern tendency in Zoogeography. According to these authors the chief aim of zoogeographical study consists—as in any other branch of biology—in the demonstration of its geological development. We have to designate this most emphatically, as the final goal of Zoogeography: the retracing of the present animal distribution to its beginning in the past, and a corollary of this is the reconstruction of the ancient physical features of the earth's surface, since these in the first place have guided the development. In the latter respect the distribution of land and water in past times is all-important and the easiest to be traced.

Thus Zoogeography becomes a very important aid not only to physical Geography itself, but also to historic Geology.

The above introductory remarks seem necessary, because the purpose and methods of the new tendency in Zoogeography have been frequently misunderstood, and especially because it was not seen that in this way the fruitless discussions on the limits and value of the different zoogeographical regions, etc., have been rendered unnecessary. Yet it is a habit among zoogeographers to create or discuss zoogeographical regions according to Wallace's ideas, and this is done not only by writers who, like Wallace and Sclater, are principally opposed to any progress in Zoogeography, but also by those who are familiar with the new ideas about the geological development of animal distribution. The old method has become an integral part of this branch of science to such a degree

that any research in this direction is deemed incomplete that is not finished by the creation or discussion of "regions."

In opposition to this, we wish to emphasize that we consider it entirely a matter of indifference whether we accept any regions or not, since none of the possible schemes can be satisfactory. Only in a very limited degree and in a modified sense we believe it advisable to divide the earth into regions, and we have proposed such a division for the marine life districts.<sup>1</sup> This scheme, however, is not intended to represent or to express the actual distribution of any animals, but it is a scheme of the distribution of the conditions of existence in the oceans of the present time without consideration of the past or of any definite group of animals. The only purpose of these regions is to single out those marine animals which correspond to the normal conditions of life and to separate them from the abnormal cases; under "*normally distributed*," consequently, we mean those animals which shape their distribution according to the present features of the earth's surface and which belong in their origin to recent time. All the rest differs and does not fit into these regions; but instead of leaving them out of consideration we know that just these cases are the most interesting, since they demand closer investigation. In most cases we find that these instances of "abnormal" distribution are to be traced back into the geological past in order to be properly understood. This latter study is the most important branch of Zoogeography, and we see that the introduction of "regions" in our method is only the means by which we discover the more interesting and important cases, but it is not the final aim.

Of course the same method may also be used for land and freshwater animals, and it may here be incidentally remarked that the regions proposed by Wallace are in this respect superior to any modifications introduced by later authors, since they generally are well limited and isolated by physical boundaries given on the surface of the earth. But if we are satisfied with the simple statement of the fact that some animals fit into these regions while others do not, we do not approach the solution of the question as to how the actual distribution originated: we are to advance one step further and investigate those cases which do not submit to the scheme. The final aim of this investigation is to compare and group together

<sup>1</sup> Ortmann, A. E., *Grundzuge der marinen Tiergeographie*, Jena, 1896.



those abnormal cases which resemble each other. Thus we gain certain general views as to ancient geography, and we are finally enabled to trace the distribution of land and water, of climatic conditions and the like in the geological past.

Most prominent among the groups of animals that are available for these investigations are the *Mammals*, and they have actually been used for just this purpose by various authors (Doederlein, Zittel, Lydekker, Scharff, Osborn). The palæontological material within this group is the most complete of all. But there is one important drawback: since the history of the *Mammals* hardly goes back beyond Tertiary times, at any rate since the palæontological record of this group is more or less complete only within the Tertiary, we can only draw conclusions from them as to the geographical conditions of this period, while we have to refrain from an investigation of those of the Mesozoic times.

This is a very different matter with the land and freshwater *Mollusks*. According to what we know, it is apparent that many of these forms can be traced back to Mesozoic times, sometimes even to Palæozoic, and, indeed, it is this group of animals that has furnished the material for the studies of von Ihering, Pilsbry, Hedley, Kobelt, and we are to expect that further investigation in this direction may yield interesting results.

Other groups have also been used. Von Ihering introduced the study of *Ants*, and there may be other promising groups among the *Insects* (for instance *Spiders*). But since the majority of the *Insects* possess unusual means of dispersal (power of flight) that are apt to obscure the original conditions of distribution, *Insects* in general are not well adapted to this kind of research. Of other animals the *Earthworms* have been studied in this respect (by Beddard), and of the Vertebrates, *Reptiles*, *Amphibians*, and freshwater *Fishes* are very likely to prove good objects, since their history in many cases goes back to the beginning of the Mesozoic or even to the Palæozoic time.

In the following treatise I wish to call special attention to certain groups of *Decapod Crustaceans* that live in fresh water. In part these have been discussed previously by other writers as well as by myself, but it is worth while to go more into detail, since we shall find them very interesting in this respect.

The following groups of freshwater Decapods are known :

FAMILY : *Atyidæ*.

*Palæmonidæ* (in part).

*Potamobiidæ*.

*Parastacidæ*.

*Ægleidæ* (monotypic).

*Potamonidæ*.

There are, scattered among other families, other forms of freshwater Decapods, but the above are the most important groups. These are found either exclusively in fresh water or possess the largest number of their members there, and are found only in rare cases in the sea.

As regards the *Atyidæ*, the present writer has collected the chorological material in a previous paper.<sup>2</sup> This is no doubt one of the oldest groups of freshwater Decapods, and their origin, as is very likely also according to their morphological characters, is to be sought for possibly in Jurassic times, although fossil forms are not positively known. The chief features of their distribution are excessively abnormal and even confusing, and therefore the extreme age of the group is again confirmed. On the other hand, there are smaller groups within this family, the distribution of which was apparently formed in later times. Since there is every reason to believe that our knowledge of the actual distribution of the *Atyidæ* is still more or less defective, we shall refrain from discussing it and refer only to the latest summary given by the present writer.<sup>3</sup>

In the family of the *Palæmonidæ* the genus *Palæmon* forms a group that possesses numerous species which are found chiefly in fresh water. Their distribution, which has also been previously investigated by the present writer,<sup>4</sup> points distinctly to the fact that this genus is a very recent one, which is at the present time just in the act of immigrating into fresh water, and that this process is by no means completed. The different species depend in their dis-

<sup>1</sup> Compare Ortmann, A. E., in Bronn's *Klassen und Ordnungen des Thierreichs*, Vol. v, 2, 1899, p. 1185. We leave out of consideration the families *Cænobitidæ* and *Gecarcinidæ*, which are more properly land animals. See *ibid.*, pp. 1183 and 1184.

<sup>2</sup> Ortmann, in *Proc. Acad. Philadelphia*, 1894, p. 397 ff.

<sup>3</sup> In Bronn's *Klassen und Ordn.*, l. c., 1901, p. 1286 f.

<sup>4</sup> In *Zool. Jahrb. Syst.*, Vol. v, 1891, pp. 744-748, and in Bronn's *Klassen und Ordn.*, l. c., 1901, p. 1291 f.



tribution largely on the conditions prevailing in the littoral waters, and generally they follow the physical regions which we have proposed for the marine littoral district of the present time. To this there are only a few exceptions, due to special means of dispersal (crossing over continental divides, for instance). For the investigation of ancient Geography this genus has no value.<sup>1</sup>

In the following we shall treat of the remaining four families: *Potamobiidæ*, *Parastacidæ*, *Ægleidæ* and *Potamonidæ*.

#### PART I. CHOROLOGICAL MATERIAL.

##### A. CHOROLOGY OF THE FAMILIES POTAMOBIDÆ AND PARASTACIDÆ. (See Fig. 1.)

##### BIBLIOGRAPHY.

##### (a) General Discussions and Systematic Revisions.

HUXLEY, TH.: *The Crayfish*, London, 1879.

FAXON, W.: "A Revision of the Astacidæ" (*Mem. Mus. Harvard*, Vol. 10, 1885).

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<sup>1</sup> Coutière, H. ("Sur quelques Macrures des eaux douces de Madagascar," in *C. R. Acad. Sci. Paris*, Vol. cxxx, 1900, pp. 1266-1268), discussing the Palæmons of Madagascar, has advanced some views as to their distribution and concludes by putting the (unanswered) question whether this distribution has formed under conditions similar to the present ones or not. This question, however, has been answered in detail by the present writer in the paper quoted above (1891), with which Coutière seems to have been unacquainted. This is also evidenced by the fact that some of the peculiarities of distribution in this genus, emphasized by the present writer, are not mentioned by Coutière—for instance, the relation of the West African species to those of America. Coutière holds that the West African (not South African) *Palæmon vollenhoveni* Herkl. is most closely allied to *P. brevicarpus* Haan from Japan, while I regard the relationship to the American *P. jamaicensis* (Hbst.) as more important.

As regards *Bithynis hildebrandti* Hlgdf. (1893) from Madagascar, I believe it is hardly possible to connect this species genetically with the type species of this genus from Chile. I think this is a case of convergency. The opinion of Coutière, that the theory of a Posttriassic connection of Madagascar with India and Africa is to be abandoned, has no support whatever. The distribution of *Palæmon*, which, according to Coutière himself, does not go back beyond Miocene times, is absolutely irrelevant to this question, and even the Miocene age of *Palæmon* seems to be doubtful. The presence of identical species on the eastern and western sides of the Cordilleras in South America is no evidence for this, since this distribution is not discontinuous, and the respective species have apparently crossed this chain of mountains, and are actually found in the mountains high up in the headwaters of the Anazonas river, for instance.

FIG. 1. Distribution of the Crayfishes of the families *Potamobitidae* and *Parastacidae*.



- FAXON, W.: "Notes on North American Crayfishes, Family Astacidae" (*Pr. U. S. Mus.*, Vol. 12, 1890).
- FAXON, W.: "Observations on the Astacidae in the U. S. National Museum and in the Museum of Comparative Zoology, with Descriptions of New Species" (*Pr. U. S. Mus.*, Vol. 20, 1898).
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- (b) *Special Literature, published after Faxon's Revisions (1885, 1890, 1898), or not embodied in them.*
- BERG, C.: "Datos sobre algunos crustaceos nuevos para la fauna argentina" (*Commun. Mus. Buenos Aires*, Vol. 1, 1900).
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- PHILIPPI, R. A.: "Dos palabras sobre la sinonimia de los Crustaceos, Decapodos, Braquiuros o jaivas de Chile" (*Ann. Univers. Chile*, 1894).

For the intended publication of the Decapods in the "Thierreich," edited by the German Zoological Society, the present writer was obliged to make a complete collection and a critical review of the systematic literature of these two families. Of course, the results of these studies are embodied in the following portion of this article, although it is not possible to refer to this work, the manuscript of which has just been finished.

#### 1. Family: POTAMOBIDÆ Huxl.<sup>2</sup>

The family *Potamobiidae* is divided into two genera: *Potamobius* Sam. and *Cambarus* Er. The latter is no doubt the more special-

<sup>1</sup> Of this rare paper I possess a handwritten copy and sketches of the figures, through the kindness of Dr. F. Philippi, of Santiago.

<sup>2</sup> Those authors (Faxon, Rathbun) who retain for the European crayfish the

ized one, and its distribution is more sharply limited than that of *Potamobius*, it being found only in the eastern parts of North America, Mexico and Cuba.

Genus: *Cambarus* Er.

The genus *Cambarus* contains at present sixty-six well-known species; of a sixty-seventh, the group to which it belongs is doubtful (*C. clypeatus* Hay, Missouri). The species form five groups within the genus.

Sixteen species belong to the first group, namely:

- |                               |                                 |
|-------------------------------|---------------------------------|
| 1. <i>blandingi</i> (Harl.).  | 9. <i>versutus</i> Hag.         |
| 2. <i>hayi</i> Fax.           | 10. <i>spiculifer</i> (Lec.).   |
| 3. <i>fallax</i> Hag.         | 11. <i>pellucidus</i> (Tell.).  |
| 4. <i>clarki</i> Gir.         | 12. <i>acherontis</i> Loennb. — |
| 5. <i>troglydites</i> (Lec.). | 13. <i>wiegmanni</i> Er.        |
| 6. <i>lecontei</i> Hag.       | 14. <i>alleni</i> Fax.          |
| 7. <i>angustatus</i> (Lec.).  | 15. <i>evermanni</i> Fax.       |
| 8. <i>pubescens</i> Fax.      | 16. <i>fenicillatus</i> (Lec.). |

Eight species belong to the second group:

- |                          |                                    |
|--------------------------|------------------------------------|
| 1. <i>cubensis</i> Er.   | 5. <i>gallinus</i> Cock. and Port. |
| 2. <i>carinatus</i> Fax. | 6. <i>gracilis</i> Bund.           |
| 3. <i>mexicanus</i> Er.  | 7. <i>carolinus</i> Er.            |
| 4. <i>simulans</i> Fax.  | 8. <i>advena</i> (Lec.).           |

To this group possibly belongs *clypeatus* Hay.

Thirteen species belong to the third group:

- |                             |                                     |
|-----------------------------|-------------------------------------|
| 1. <i>acuminatus</i> Fax.   | 8. <i>uhleri</i> Fax.               |
| 2. <i>bartoni</i> (Fabr.).  | 9. <i>setosus</i> Fax.              |
| 3. <i>longulus</i> Gir.     | 10. <i>extraneus</i> Hag.           |
| 4. <i>latimanus</i> (Lec.). | 11. <i>jordani</i> Fax.             |
| 5. <i>dubius</i> Fax        | 12. <i>cornutus</i> Fax.            |
| 6. <i>diogenes</i> Gir.     | 13. <i>hamulatus</i> Cope and Pack. |
| 7. <i>argillicola</i> Fax.  |                                     |

generic name of *Astacus* M. E., claim that Latreille (Consider. génér., etc., 1810; see Faxon, 1898, p. 662) has made this species, *Astacus fluviatilis* Fabr., the type of the genus *Astacus* Fabr. This statement of Latreille, however, is erroneous, since *Astacus* of Fabricius is a genus without type, and remained such until Samouelle (*The Entomologists' Useful Compendium*, 1819, p. 95) separated *Astacus* and *Potamobius* (Lobster and Crayfish). See Faxon, 1885; Ortmann, "Das System der Decapodon Krebse" (*Zool. Jahrb. Syst.*, Vol. 9, 1896, p. 430), and Stebbing (in *Natural Science*, Vol. 12, 1898, p. 239 ff.).



Twenty-six species belong to the fourth group :

- |                                 |                               |
|---------------------------------|-------------------------------|
| 1. <i>mississippiensis</i> Fax. | 14. <i>virilis</i> Hag.       |
| 2. <i>immunis</i> Hag.          | 15. <i>nais</i> Fax.          |
| 3. <i>medius</i> Fax.           | 16. <i>pilosus</i> Hay.       |
| 4. <i>lancifer</i> Hag.         | 17. <i>longidigitus</i> Fax.  |
| 5. <i>palmeri</i> Fax.          | 18. <i>sloanei</i> Bund.      |
| 6. <i>difficilis</i> Fax.       | 19. <i>rusticus</i> Gir.      |
| 7. <i>alabamensis</i> Fax.      | 20. <i>meeki</i> Fax.         |
| 8. <i>compressus</i> Fax.       | 21. <i>harrisoni</i> Fax.     |
| 9. <i>propinquus</i> Gir.       | 22. <i>forceps</i> Fax.       |
| 10. <i>neglectus</i> Fax.       | 23. <i>spinusus</i> Bund.     |
| 11. <i>diguetti</i> Bouv.       | 24. <i>erichsonianus</i> Fax. |
| 12. <i>affinis</i> (Say).       | 25. <i>putnami</i> Fax.       |
| 13. <i>indianensis</i> Hay.     | 26. <i>hylas</i> Fax.         |

Three species belong to the fifth group :

- |                            |                          |
|----------------------------|--------------------------|
| 1. <i>montezumæ</i> Sauss. | 3. <i>shufeldti</i> Fax. |
| 2. <i>chapalanus</i> Fax.  |                          |

In discussing the distribution, it is best we take up the single groups. The species of the *first group* are restricted chiefly to the southern parts of the United States and Mexico, and we observe that all, with two exceptions (*blandingi* and *pellucidus*), are found in the region of North America formed by Mexico, Texas, Louisiana, Mississippi, Alabama, Florida, Georgia and South Carolina. *C. blandingi* possesses the widest range; in the States named it is wanting only in the farthest southeast, in Florida and Georgia<sup>1</sup>; but on the other side it extends beyond those limits along the Atlantic coast, passing through North Carolina, Maryland and New Jersey into the neighborhood of New York, and in the Mississippi-Ohio basin it extends northward through Arkansas, Tennessee, Missouri, Illinois and Indiana into Ohio and southern and eastern Iowa. Westward, it has been found as far as Indian Territory. *C. pellucidus* is a blind cave species which is restricted to certain localities in Indiana and Kentucky.

It is apparent that the centre of this group is in the Gulf States and in the southern Atlantic States, while the region of the eastern mountains (Allegheny system) is left unoccupied by it, and only one species advances northward along the Atlantic coast and in the

<sup>1</sup> It is very likely to be discovered in Georgia.

Mississippi valley to the neighborhood of the Great Lakes. To this latter extension of the range also belongs *C. pellucidus*. Southward, this group goes through Texas (here it has been found near the Mexican boundary line), and is found in the neighborhood of the city of Mexico (*C. wiegmanni*). Whether this latter locality is connected with the localities in Texas or not is unknown.

The centre of distribution of the *second group* is to be found in the Southwest. We know two species from Mexico, two from New Mexico, Texas and Kansas. Another species (*C. gracilis*) extends from these parts northward (in the prairies), and is found in Kansas, Iowa, Illinois, as far as Wisconsin. In the South we have, more or less isolated, *C. clypeatus* in Mississippi, and absolutely isolated are *C. carolinus* and *advena* in South Carolina and Georgia and *C. cubensis* in Cuba.

Within this group we observe a very striking *discontinuity*; not only the Mexican localities are separated from those in the United States, but also in the Gulf States, the southern Atlantic States and in Cuba there are representatives of this group, separated from the rest in the Southwestern and Central States.

Very different is the range of the *third group*. Here we have complete continuity, and the centre is evidently in the system of the Allegheny mountains and in the East. The species are very numerous in the mountainous parts of Tennessee, Kentucky, North Carolina, Virginia and West Virginia, Maryland, Pennsylvania, and in the adjoining parts of Ohio and Indiana. This group is also well represented in Illinois, and extends, gradually decreasing in density, westward into Wisconsin, Minnesota, Iowa, Missouri (in the eastern part only), Arkansas and the Indian Territory. It is very rare in Texas, Louisiana, Mississippi; is slightly represented in Alabama, Georgia and South Carolina, but is wanting in Florida. In a northeasterly direction, a single species (*C. bartoni*) extends over New York and New England across the Canadian boundary into New Brunswick, where it reaches the Restigouche river, a tributary of the Gulf of St. Lawrence. The same species is found in the northern affluents of Lake Ontario (Toronto) and the St. Lawrence river in Quebec (St. John's Lake), where it marks the northern boundary of the genus. In Michigan this group is represented in the neighborhood of Lake Huron, but it has not been found north of the Great Lakes in Canada. The northeastern extension of the range of this group, on the one hand, is very



remarkable, while, on the other hand, we have a scarcity of it south of the Allegheny system and west of the Mississippi. With the exception of one isolated station of *C. argillicola* in Texas, this group is not represented in the Southwest.

The largest number of species is found in the *fourth group*. In certain respects it corresponds, in its distribution, to the third, namely, in its exceeding scarcity in the South and Southwest. It is wanting in Florida, in the low parts of the Carolinas, of Georgia, Alabama and Mississippi. It is also wanting in Louisiana, and in Texas it is found only in the northeastern corner (near the boundaries of the Indian Territory and Arkansas). Beginning here, it extends northward over the Mississippi-Missouri-Ohio basin, becoming more abundant, the centre being situated, in this region, in the States of Missouri, Tennessee, Kentucky, Indiana, Illinois, Iowa and the southern parts of Michigan and Wisconsin. Eastward this group enters Ohio, Pennsylvania, Virginia, Maryland, New Jersey and New York, reaching its northeastern limit north of Lake Ontario, near Toronto and Montreal. In Wisconsin it extends to Lake Superior, and one species (*C. virilis*) reaches from Minnesota, including the northeastern corner of North Dakota, to Lake Winnipeg and the Saskatchewan river, the most northern locality known for the genus. Westward, the range of this group includes Kansas and Nebraska (southern and eastern part only) and the southeastern corner of Wyoming: this is the most advanced point for the genus in a northwesterly direction. Entirely isolated from the range of this group, thus far described, we find a species (*C. digueti*) in Mexico (Pacific side, State of Jalisco), and another species (*C. immunis*, known from the prairies of Michigan, Indiana, Illinois, Wisconsin, Iowa) is said to be present near Orizaba, Mexico.

Therefore we may say, generally, that the centre of this group is situated in the central part of the United States, about in that region where the three large rivers, Missouri, Mississippi and Ohio, unite. Thence it extends into the eastern and southeastern mountains, but hardly across them; northward, it reaches the St. Lawrence and the Saskatchewan rivers and westward Wyoming. In a southwesterly direction it hardly reaches Texas, and the Mexican localities seem to be isolated from the rest.

Of the three species of the *fifth group*, two are found in Mexico and one near New Orleans.

Taking together the distribution of the five groups, we find that the range of the genus *Cambarus* extends over the following parts of North America: In Mexico, the respective species are reported from the following States: Vera Cruz (near Vera Cruz and Orizaba), Pueblo, Mexico, Michoacan. This line would represent the southern boundary of the range.<sup>1</sup> Further, the genus has been found in the States of Jalisco and Sinaloa (Mazatlan) (in the drainage of the Pacific Ocean); on the central plateau, in Guanajuato, San Luis Potosi (Santa Maria) and Coahuila (Parras). This latter locality forms in a certain degree the connection of the Mexican part of the range of the genus with that of the United States, since the Mexican State Coahuila extends northward to the Rio Grande del Norte, and just across this river, on its left bank, there is, in Kinney county, Texas, a locality for *C. clarki*. Thence the range of the genus is apparently continuous, and reaches eastward to the sea (Gulf of Mexico and Atlantic Ocean).<sup>2</sup> Toward the west and north it is circumscribed by the following line: from Kinney county, Texas, to New Mexico (including its eastern part), then receding toward Indian Territory and leaving out Oklahoma, farther, including Kansas, the southeastern corner of Wyoming (possibly a part of Colorado), the southern and eastern part of Nebraska, crossing here the Missouri, including Iowa and Minnesota and possibly parts of the Dakotas, at any rate the northeastern corner of North Dakota, crossing over into Canadian territory and including the region of Lake Winnipeg and Saskatchewan river (northernmost point). Thence this line recedes in a southeasterly direction, reaches Lake Superior, and follows the Great Lakes as far as Lake Erie. At Lake Ontario it advances again northward and follows at a certain distance the St. Lawrence river, reaching at the Lake St. John in Quebec the northernmost point in the East. Then it turns southward, crosses the St. Lawrence and includes, in New Brunswick, the drainage of the Restigouche and Miramichi rivers (emptying in the St. Lawrence Gulf) and also the St. John river (emptying in the Bay of Fundy). Thus the largest part of New Brunswick seems to belong to the range of this genus, while

<sup>1</sup> The genus is said to be represented near Alta Vera Paz, in Guatemala (Faxon, 1885, p. 173). This would advance the range southward beyond the Isthmus of Tehuantepec. This locality, however, needs confirmation.

<sup>2</sup> In Florida, only in the northern half are localities known, southward as far as Orange, Lake and Hillsboro counties.



Nova Scotia is excluded. Isolated from the continuous Mexican and United States ranges is the Island of Cuba, where *C. cubensis* has been found.

It is hard to say where the centre of the whole genus is situated. Judging from the number of species represented in the different parts, it seems to be more in the East than in the West, but for the rest the genus is pretty evenly distributed in the Southeastern States, in the region of the Alleghanies and the central basin, and decreases markedly only in a westerly direction, disappearing before it reaches the foothills of the Rocky Mountains. In the Southwest, in Texas and New Mexico, the genus is less abundant, and in northern Mexico it is found only near Parras, in the State of Coahuila; but then again it becomes more abundant in the central part of Mexico. Whether this apparent scarcity in northern Mexico and Texas corresponds to the actual conditions, or whether it is due to defective knowledge of these parts, cannot be decided. One result, however, is very evident: the genus is preëminently characteristic of the central and eastern parts of the United States, there attaining its highest development as regards the number of species.

Now, what is the origin of this distribution of *Cambarus*? Did this genus originate in these parts, or whence did it come, and which are its ancestors?

In order to answer the first question, we learn much by recalling to our mind the distribution of the single groups as stated above. We have seen that the centre of the first group is in the Southeast; the range of the second group—although somewhat discontinuous—centres in the Southwest. The third group has evidently its centre in the mountainous regions of the Allegheny system, the fourth group in the central basin and the fifth in Mexico.

The second and fifth groups are strongly represented in the Southwest, the first group has distinct relation to these parts, the fourth group only a few isolated stations, while the third group is entirely wanting there.<sup>1</sup>

<sup>1</sup> Faxon (1885, p. 178) expresses this in the following way: in the South (Mexico, Cuba, Gulf States and Atlantic States south of North Carolina) species of the first, second and fifth groups prevail, while comparatively few species of the third and fourth groups are present; in the North (Atlantic States north of South Carolina, Central States and Canada) species of the third and fourth groups prevail, while only a few species of the first and second advance into the northern provinces.

As regards the morphological relations of the five groups, we are to consider first Faxon's view (1885, p. 19), that the species of the first group are morphologically the most primitive ones. He draws this conclusion chiefly from the shape of the male copulatory organs. If we compare, however, certain species of the second group (*simulans*, *mexicanus*, *cubensis*) with those of the first group in this respect, we see that they chiefly differ from the latter only in the smaller number of hooks on the pereiopoda of the male (only on the third pair, not on the third and fourth, as in the first group). On this account I should prefer to regard the species named as the most primitive forms of the genus, although, on the other hand, I agree with Faxon (1885, p. 47) in believing that the other species of the second group more nearly approach the third group. That the third and fourth groups, compared with the others, are more advanced forms is also my opinion. As the most specialized species I regard those of the third group which have acquired burrowing habits (*diogenes*, *argillicola*, *dubius*). The species of the fifth group differ from all the rest in the presence of hooks in the second and third pereiopods of the male, and thus I think they represent an early separated side branch. The copulatory organs of the male in this group resemble in certain respects more those of the first and second groups than those of the third and fourth, and the more primitive character of these species is also suggested by the general shape of the body.

Thus we see that the more primitive forms of the first, second and fifth groups belong chiefly to the South and point distinctly to a connection with Mexico, while among the more advanced and specialized forms of the third and fourth groups this latter connection is hardly expressed or not at all. Their origin and main distribution belong to the more northern parts.

*This points to an origin of the genus in the Southwest, and we believe that the genus came from Mexico and immigrated into the United States in a northeasterly direction.*

A few additional distributional facts tend to support this conclusion. It seems that in those groups which possess a large representation in the Southwest the distribution is rather discontinuous. This is most evident with the second group. Now discontinuity in distribution of any animal is very often a sign of the breaking up of a former continuous range by unfavorable physical conditions. In the present case it appears that at a certain time the immigra

tion of *Cambarus* from Mexico into the United States did not meet with serious obstacles, but that later in the intermediate regions (northern Mexico and Texas) more unfavorable conditions arose which separated the United States more distinctly from Mexico, and this is possibly due to a more decided development of the desert character of these parts. Thus the Mexican representatives of the first, second, fourth and fifth groups became more or less separated from those in the United States, the first and fourth groups developed more abundantly in the United States, while the third originated there, possibly out of the second group, which in these parts did not make any marked progress and was suppressed and restricted to a few more or less isolated stations, probably on account of its primitive character. An interesting light is thrown upon this question by the presence of one species of the second group (*C. cubensis*) in Cuba. This species is closely related to *C. mexicanus* (Pueblo, San Luis Potosi), while it has no closer relations in the United States, and thus its Mexican origin is most distinctly indicated. Therefore we may safely say of the second group that it is a very primitive one and that Mexico, not the United States, is to be taken as its centre of origin.

The character of discontinuity is more or less noticeable also in the southwestern part of the range of the first, fourth and fifth groups. The first possesses an isolated species (*wiegmanni*) in Mexico, and the stations of *C. blandingi* and *clarki* in Texas are very scattered. In the fourth group we have an isolated species (*digueti*) in Mexico (Jalisco), while *C. immunis*, a species found elsewhere in the northern central basin, has been reported from Orizaba, in Mexico.<sup>1</sup> The fifth group has two species in Mexico and, widely separated from them, a third near New Orleans. If we compare with this the northern part of the ranges of the first, third and fourth groups we see everywhere perfect continuity. In every direction from the centre, except toward the Southwest, the intensity of distribution decreases gradually. This is especially true for the first group, the centre of which is in the Southern States, in the directions northward along the Atlantic coast and upward in the Mississippi Valley. In the third group, whose centre is in the Allegheny system, there is a regular decrease in intensity in all directions, and in the fourth group a very regular decrease is

<sup>1</sup> We have to accept this record, however, very cautiously.



noticeable from its centre in the middle Mississippi basin toward the East, North and West.

Thus we are to recognize the fact that the different groups, chiefly the first, third and fourth, express in their distribution a regular, continuous advance in a northeasterly direction. Toward the North and East is continuity, which represents a more recent stage in distribution, while in the opposite direction, toward Southwest, we observe discontinuity, which characterizes generally a more ancient stage. In the second group we have a very remarkable discontinuity, and this group is a comparatively primitive one, and the fifth group, which is also primitive in some degree, is chiefly found in the Southwest.

All the foregoing considerations tend to justify our conclusion that the migration of the genus *Cambarus* into the United States started in the Southwest, on the Mexican plateau, and advanced in a northeasterly direction.

Taking up now the second point to be considered, the question of the origin and the ancestral forms of the genus *Cambarus*, we shall be satisfied—for the present—with the opinion of Faxon (1885, p. 16), which is also that of the present writer, that this genus is the most highly specialized within the family *Potamobiidae*, a corollary of which is that it must have originated from forms of a lower type, which probably corresponded to the genus *Potamobius*; in fact, it is easy to imagine that *Cambarus* is derived directly from *Potamobius* by the suppression of the single posterior pleurobranchia and the high specialization of the copulatory organs. However, before entering into a more detailed discussion of the relation of *Cambarus* and *Potamobius*, we shall give a sketch of the chorology of the latter genus.

#### Genus *Potamobius*.<sup>1</sup>

It is advisable here to go more into detail, since, on the one hand, a synopsis of the more recent publications in this group is desirable, and since, on the other, the number of species in this genus is comparatively small and our knowledge of them excellent. The genus is divided into two subgenera: *Potamobius* sens. strict. Ortm. (*Astacus* sens. strict. Fax.) and *Cambaroides* Fax.

<sup>1</sup> The following facts have not been put together since Faxon's review (1885). I shall use here chiefly the revision of this group which I have prepared for the "Thierreich."

Subgenus *Potamobius*—twelve species:

European group:

1. *pallipes* (Lereb.). South and West Europe: Central Spain, France, England, Ireland, Southwest Germany, Italy southward to Naples, Dalmatia, Greece.
2. *torrentium* (Schrk.). Central Europe: Switzerland, South Germany, Bohemia.
3. *astacus* (L.). West Russia (northward to Finland), Austria, Germany, Denmark, South Sweden and Norway (possibly introduced), France, southward to Northern Italy.
4. *leptodactylus* (Eschz.). Ponto-Caspian basin: Hungary (Danube, Theiss), South and Central Russia, northward to the White Sea; in Siberia in the region of the Caspian Sea. Further, in West Siberia in the basin of the rivers Obi and Irtysh, introduced, as reported, but possibly indigenous (see Faxon, 1885, p. 151).
5. *pachypus* (Rthk.). Estuaries of the Black and Caspian Seas.
6. *colchicus* (Kessl.). Transcaucasia (upper Rion river).
7. *kessleri* (Schimk.). Turkestan (Sir Darja).

American group:

8. *leniusculus* (Dan.). Washington, Oregon (lower Columbia river), California (San Francisco).
9. *trowbridgei* (Stps.). Washington, Oregon (lower Columbia river).
10. *nigrescens* (Stps.). California (San Francisco), Washington, Alaska (Unalaska).
11. *klamathensis* (Stps.). British Columbia (east of Cascade Mountains), Idaho, Washington, Oregon, Northern California (mountain rivers).
12. *gambeli* (Gir.). In the Rocky Mountains: on the Pacific slope in Utah, Idaho, Wyoming and Yellowstone Park; on the Atlantic slope; mouth of Yellowstone river (eastern State line of Montana).

Subgenus *Cambaroides*—four species:

1. *schrenki* (Kessl.). Lower river Amur.
2. *dauricus* (Pall.). Upper river Amur.
3. *japonicus* (Haan). North Japan: Yesso.
4. *similis* (Koelb.). Korea.

Generally speaking the range of the genus *Potamobius* exhibits a striking *discontinuity*, which has often been discussed. One group of species occupies a continuous area in *Europe* (and Western Asia); another in *East Asia*; a third in Western *North America*.<sup>1</sup> It has been said that it is another remarkable fact that the American species resemble the European more than they do the East Asiatic, and that the latter more approach *Cambarus*, which idea is expressed by their position in a separate subgenus named *Cambaroides*. But as regards the gills and the general form of the body,<sup>2</sup> *Cambaroides* belongs without question to *Potamobius*. The male copulating organs are as different from those of *Cambarus* as they are from those of the typical species of *Potamobius*, and the only character that points decidedly to *Cambarus* is the presence of copulatory hooks on the ischiopodites of certain peræopods. But also in this respect *Cambaroides* is rather peculiar, since these hooks are found on the second and third pair, which case is represented among *Cambarus* only in the fifth group (containing only three species), while all the rest of the numerous species of this genus possess these hooks either on the third and fourth or only the third pair.

I am of the opinion that the resemblance of *Cambaroides* to *Cambarus* does not express very close blood relationship, but is due to convergency. The development of hooks on the peræopods of the male, which serve, as is now known, the purpose of taking hold of the female in copulation, is easily understood, if we remember the manner in which copulation is performed, and it is also easily intelligible that this device has possibly developed independently in *Cambaroides* and *Cambarus*. The shape of the copulating organs, which shows no doubt in *Cambaroides* a certain similarity to the *Cambarus* type, can be explained in the same way, since it is quite clear that if they are used in the same manner they may

<sup>1</sup> To the latter area belongs an isolated locality of *P. nigrescens* in Alaska. According to Hay (1899) this species is found all along the western coast of North America, from California to Alaska. To my knowledge intermediate localities between Washington and Alaska have not been published.

<sup>2</sup> Faxon (1885, p. 126) calls the shape of the body "subcylindrical," and says that it resembles that of *Cambarus*. I cannot concur with him in this opinion; the form of the carapace in *Cambaroides* is decidedly rather oval, as in *Potamobius*, and besides there are variations also in this respect within the genus *Cambarus*.



assume the same or a similar form. If, finally, Faxon says that the shape of the chelæ in *Cambaroides* resembles those of *Cambarus*, he means apparently only the general weak development of them, and we must bear in mind that many *Cambari* are more like typical *Potamobii* in this respect.<sup>1</sup>

Thus the view seems supported that *Cambaroides* is not so very closely related to *Cambarus*, as has been hitherto supposed, and that the similarities which were emphasized are due only to convergence. If we peruse the comparison of the characters of *Cambaroides*, *Potamobius* and *Cambarus* given by Faxon (1885, pp. 126, 127), we find that *Cambaroides* is in some of them more isolated, and that it resembles in others even more the West American species of *Potamobius*. (For instance, the lack of a transverse suture of the telson; the shape of the second male abdominal appendage; the lack of the first abdominal appendage in the female.)

The conclusion drawn from the foregoing is that in certain respects (telson, second pleopods of male, first pleopods of female) *Cambaroides* represents a type that points to the West American *Potamobii*, while the European species are more divergent from it, and there is nothing that opposes the view that this subgenus (which might as well be regarded as a separate genus) forms the starting point on the one side for the European *Potamobii* and on the other for the American *Potamobii*, while subsequently it has changed itself and become different from both (in the male copulatory organs).

The subgenus *Cambaroides* is restricted to the northeastern parts of Asia (region of Amur river, Korea, North Japan). The exact boundaries of its range have nowhere been located positively, and it is not impossible that in the Siberian and northern Chinese mountains other representatives of it may exist. For the present the area from which species of *Cambaroides* are known is absolutely separated from the European area of *Potamobius*.

As regards the latter, its centre is apparently in Southern and Central Russia. From these parts the different species extend into Western Europe, southward to Central Spain, Middle Italy and Greece, and in Russia one species passes southward across the Caucasus Mountains. Eastward a species is found as far as Turke-

<sup>1</sup> Some other characters of *Cambaroides* indicate that this subgenus differs from *Potamobius* as well as from *Cambarus*, and these are characters which approach it to the crayfishes of the southern hemisphere. Compare below.

stan, and northward the area reaches the White Sea. East of the Ural Mountains the genus is said to be lacking, but it is found (the widely-distributed species *P. leptodactylus*) introduced in the river Obi and its affluents. Some observations, however, have been made which render it possible that *P. leptodactylus* is an original inhabitant of these parts.

As Huxley (1879) and Faxon (1885, p. 140) believe, the different forms of *Potamobius* have immigrated into Europe from the East, and we can distinguish an older immigration on the part of the group formed by the species *P. pallipes* and *torrentium* and a more recent one on the part of *P. astacus* and its allies. And even within the latter group it seems that *P. astacus* is older than the other species and that it is pushed gradually westward by *P. leptodactylus*, which is spreading in a westerly direction. The writer is of the same opinion, and we shall see below that this is the only theory that is admissible, if we consider the origin of Europe as a continental mass. The occupation of Europe, after it had lost the character of an archipelago and become part of the Eurasiatic continent, was possible for these animals only in a west-easterly direction. This corresponds also to the fact that those forms allied to the European *Potamobii*, which are the nearest geographically, are found to the east of them. They are the forms of *Cambaroides* in Eastern Asia, and we can readily imagine that from the area of distribution of *Cambaroides* an extension existed formerly in a westerly direction across Central Asia, which connected with the European area of *Potamobius*, and this connection represents the direction of the migration.

The forms of *Potamobius* which are found in Western North America possess a continuous area of distribution<sup>1</sup> which is separated from the rest of the genus. Huxley and Faxon, as has been mentioned above, believe that these American species are more closely related to the European, but I think we have reason to accept a different view.

My opinion is that a primitive group, which was ancestral to all three of the living groups, formerly existed in Eastern Asia, which is to be regarded as the centre of origin of the *Potamobiidae*. This group sent out a branch in a westerly direction, which finally reached Europe, and it also sent out a branch in an easterly direction, which migrated apparently along the northern shores of the

<sup>1</sup> Possibly with the exception of the isolated station near Unalaska.

Pacific Ocean and finally immigrated into Northwestern America. A trace of the direction of this route is preserved in the presence of *Potamobius nigrescens* near Unalaska. After the final geographical separation of the European and American descendants from the original group in Eastern Asia each of the three groups developed independently, and the Asiatic group acquired several more advanced characters (copulatory organs and hooks) which otherwise are found only in *Cambarus*, but which do not point to a closer affinity to the latter genus, but are only due to parallelism.

Further, the West American *Potamobii* possess a character that is found also in *Cambarus*. Faxon mentions that the second pleopods of the male resemble not only those of *Cambaroides*, but also those of *Cambarus*, while the European species are different in this respect. This would bring the genus *Cambarus* into closer relation to the West American *Potamobii*, and although this similarity would hardly be of much value by itself, we have to regard it as significant, since it agrees well with the distributional facts. The tracing back of *Cambarus* to *Cambaroides* is geographically impossible, and just this latter difficulty has induced the writer to examine more closely the supposed resemblance of both, and the result is as has been discussed above. A closer connection of the European species of *Potamobius* with *Cambarus* is out of the question,<sup>1</sup> and thus only the third group is left, the West American *Potamobii*.

From the latter group *Cambarus* is very sharply distinguished though and no transitional forms are known. Probably this is due to the fact that the connection of the area of both is far remote geologically—that is to say, that the migration of *Potamobius* into Mexico is very old and that the separation of both genera took place in very early times, the one becoming restricted to Northwestern America (southward to California), the other developing on the Mexican plateau out of the old *Potamobius* stock that originally immigrated thither from the North. Thus the differential characters of *Cambarus* became well fixed and no transitions to the old stock are found any more.

Thus for the family of the *Potamobiidae* we may express the fol-

<sup>1</sup> Faxon (1885, p. 176) thinks that in former times *Cambarus* and *Potamobius* occupied about the same area, and in order to support this he mentions the supposed existence of a blind *Cambarus* in the caves of Carniola, Austria. However, this latter record is entirely erroneous. There exists no *Cambarus* in the caves of Carniola (see Haman, *Europäische Höhlenfauna*, 1896).



lowing opinion as to the origin of its distribution, founded exclusively upon systematic and chorological studies.

The oldest home of the *Potamobiidæ* and their centre of origin is somewhere in Eastern Asia. This ancestral stock spread chiefly in two directions: a western extension of the range crossed Central Asia, finally reaching Europe, while an eastern extension went across Bering Strait and reached the western parts of North America. The continuity of this wide area, which was once wholly occupied by the genus *Potamobius*, was interrupted subsequently in Central Asia and where there is now Bering Sea, and thus three isolated areas were formed—in Europe, in Eastern Asia and North-west America. In each one of these parts the genus *Potamobius* continued to develop separately. From the West American stock of *Potamobius* finally issued the genus *Cambarus*, which probably originated in Mexico and thence invaded the central and eastern parts of North America. The origin of *Cambarus* probably lies far back in time, since it shows no marked special affinities to any of the three groups of *Potamobius*, and probably it was separated from the latter genus before it was divided up into those three groups.

## 2. Family *Parastacidæ* Huxl.

A systematic revision of this family has not been published hitherto. The present writer has tried to collect the necessary data for a review in the "Thierreich," and although it is not possible to give a complete synopsis, based upon careful criticism of the existing descriptions as well as upon actual specimens, he has obtained a fair general idea of the various forms which make up this family.

According to these studies the present state of our knowledge of the distribution of this group is the following:

### 1. Genus *Cheraps* Er. em. Huxl.

Species:

1. *quinquecarinatus* (Gr.). West Australia: Swan river.
2. *quadricarinatus* Mrts. North Australia: Cape York.
3. *bicarinatus* (Gr.). North and East Australia: Port Essington, Cape York, Rockhampton, Burnett river, Sydney, Melbourne, Murray river.
4. *preissi* Er. Southeast Australia: Victoria.

Doubtful species: *australiensis* (M.-E.). Sydney.<sup>1</sup>

2. Genus *Astacopsis* Huxl.

Species:

1. *franklini* (Gr.). N. S. Wales and Tasmania.
2. *serratus* (Shaw). N. S. Wales: Murray river, Murrumbidgee river, Richmond river, Brisbane Water and Paramatta river near Sydney.

The following species represent probably young stages of *A. serratus*: *paramattensis* Bate and *sydneyensis* Bate, both from Sydney.

Doubtful species: *tasmanicus* Er. Tasmania.

3. Genus *Engæus* Er.

Species:

1. *fossor* Er. Tasmania.
2. *cunicularius* Er. Tasmania.

4. Genus *Paranephrops* White.

Species:

1. *planifrons* White. New Zealand, North Island and northern part of South Island.
2. *zealandicus* (White). New Zealand, South Island: Dunedin, Oamaru (Otago).
3. *setosus* Hutt. New Zealand, South Island: Canterbury.

This genus possibly is also represented in the Fiji Islands (Huxley).

A doubtful genus, which perhaps belongs in this neighborhood, is genus *Astaconephrops* Nobili.

Species:

1. *albertisi* Nobili. Southern New Guinea: Katau.

5. Genus *Parastacus* Huxl.

Species:

1. *pilimanus* (Mrts.). Southern Brazil: Rio Grande do Sul. Northern Argentina: Provinces Corientes, Entrerios, Catamarca.

<sup>1</sup> By Nobili (1899, p. 246) this species is classified with *Astacopsis*, and is recorded from the Island of Sorong, west end of New Guinea. It is very doubtful whether this is correct.

2. *brasiliensis* (Mrts.). Southern Brazil: Rio Grande do Sul.
3. *hassleri* Fax. Chili: Talcahuano, Tumbez.
4. *defossus* Fax. Uruguay. Brazil: Rio Grande do Sul.<sup>1</sup>
5. *saffordi* Fax. Uruguay. Brazil: Rio Grande do Sul.<sup>1</sup>
6. *varicosus* Fax. Reported from Colima, Mexico.<sup>2</sup>
7. *nicoleti* (Phil.). Chili: Tumbez.
8. *agassizi* Fax. Chili: Talcahuano, Llanquihue (Puerto Montt), Tumbez. Argentina: Lake Nahuel Huapi.<sup>3</sup>

Doubtful species: *chilensis* (M.-E.), *spinifrons* (Phil.), *bimaculatus* (Phil.), all three from Chili.

This genus is also found in Sta. Catharina, Southern Brazil, according to Fr. Mueller.

#### 6. Genus *Astacoides* Guér.

Species:

1. *madagascariensis* (M.-E.). Madagascar.

As regards the detailed limits of the range of the single species and genera we are very poorly informed, and, further, it is quite possible that our knowledge of the Australian and South American crayfishes is very incomplete also on the systematic side, and it is very likely that there are many unknown species.

It is evident at the first glance, however, that the distribution of the *Parastacidae* is divided into four absolutely isolated areas: Australia (including Tasmania and possibly New Guinea); New Zealand; part of South America; Madagascar. Within each of these areas are peculiar genera: in Australia, *Cheraps*, *Astacopsis*,

<sup>1</sup> I have received these two species, *defossus* and *saffordi*, from Rio Grande do Sul through Dr. H. von Ihering.

<sup>2</sup> This locality most emphatically needs confirmation. It is very surprising that this species has never been rediscovered anywhere in Mexico, although large collections of freshwater Crustaceans from these parts have lately reached the United States Museum.

<sup>3</sup> Through Prof. W. B. Scott, of Princeton, I have received from the La Plata Museum two males and one female of this species from this locality which agree well with the description, with the exception that in the larger (adult) male the right (larger) chela is more elongate, with almost parallel margins, and that the squamiform granules of it are more strongly marked. The smaller male and the female agree perfectly with *P. agassizi*.

The lake Nahuel Huapi is situated in the Cordilleras, at the southern extremity of the Argentinian province Neuquen. It drains into the Atlantic through the river Limay Leofu, which finally forms the Rio Negro. This locality is directly east of Llanquihué, in Chili, but on the opposite slope of the Cordilleras.



*Engæus*; in New Zealand, *Paranephrops*; in South America, *Parastacus*; in Madagascar, *Astacoides*. All these forms are more or less closely related to each other, only *Astacoides* from Madagascar is rather isolated morphologically, since its branchial formula shows peculiar reductions (only one pleurobranchia on the fifth segment of the thorax, while in all the rest four pleurobranchiæ are present). In this respect *Astacoides* resembles the *Potamobiidæ* of the northern hemisphere.

If it should prove to be correct that the genus *Astaconephrops* of Nobili, from Southern New Guinea, as its author believes, is most closely related to the New Zealandian *Paranephrops*, this, together with the occurrence of *Paranephrops* in the Fiji Islands reported by Huxley, would indicate a distinct direction of the communication between New Zealand and the rest of the world. This would have been over the Fiji Islands in the direction toward New Guinea. As to the connection of the South American *Parastaci* with the rest of the family, we have hardly any systematic or chorological facts which permit more detailed conclusions. We can only venture to express the opinion that some kind of a connection between South America on the one side and Australia or New Zealand on the other must have once existed.

In order to get an adequate idea as to the geographical relations of the genus *Astacoides* we have to recall to our mind a few facts concerning the morphological relations of the *Parastacidæ* and the *Potamobiidæ* (see Ortmann, 1901, p. 1289). According to Faxon (1885, p. 126 f.), among the crayfishes of the northern hemisphere it is only the subgenus *Cambaroides* which approaches those of the southern. Not only the characters mentioned above, the absence of a suture on the telson and the absence of the first pleopods in the female, are common with the southern forms, but there is also a peculiarity in the arrangement of Leydig's olfactory organs on the external flagellum of the antennules which is found in *Cambaroides* as well as in the *Parastacidæ*. Moreover, if we consider the fact that among the *Parastacidæ* it is just the genus *Astacoides* from Madagascar which shows, in the branchial formula, a similarity to the *Potamobiidæ* (although in other respects the gills are peculiarly developed), it is easy to imagine, in trying to construct a connection between both families—and such a connection must have once existed—that this was located between the area of *Cambaroides* (Northeast Asia) and that of *Astacoides* (Madagascar). This would

be over India and China, generally over Southern and Eastern Asia. Under this assumption, that crayfishes formerly existed in Southeastern Asia, it also becomes clear by which way the rest of the *Parastacidae* were geographically connected with the *Potamobiidae*, namely, by way of the Indian Archipelago, from the continent of Asia over the Sunda Islands, New Guinea to Australia.

Looking over the various connections between the different isolated areas of distribution of the different groups of crayfishes, which have been suggested by the above chorological and systematical discussions, we may itemize them in the following way:

1. A connection of East Asia with North America by way of Bering Sea.
2. A connection of Cuba with Central America (Mexico).
3. A connection of New Zealand with Australia, possibly over the Fiji Islands and New Guinea.
4. A connection of Australia or New Zealand with South America.
5. A connection of Southeastern Asia with Madagascar and with Australia.

We need further explanation of the following remarkable facts:

1. The absence of *Potamobiidae* in Central Asia.
2. The absence of crayfishes in Southeastern and Eastern Asia.
3. The remarkable geographic restriction and isolation from each other of the crayfishes of the genera *Potamobius* and *Cambarus* in North America.
4. The remarkable boundaries of the area of *Parastacus* in South America.

#### B. CHOROLOGY OF THE FAMILY ÆGLEIDÆ<sup>1</sup> (See Fig. 2).

Here we shall leave for the present the crayfishes of the families of the *Potamobiidae* and *Parastacidae* and shall take up the small group formed by the *Ægleidae* of Dana. This seems to be a monotypic family, consisting only of one genus and one species, *Æglea lævis* (Latr.). The following localities are recorded for it:

Chili: Valparaiso, and between Valparaiso and Santiago; Lake Llanquihué, near Puerto Montt.<sup>2</sup> Argentina: Provinces Jujuy

<sup>1</sup> See Ortmann, 1901, p. 1290.

<sup>2</sup> Doflein, *F. SB. Akad. Muenchen*, V. 30, 1900, p. 135.

(this is the northernmost point, near the Bolivian boundary), Tucuman, San Luis,<sup>1</sup> Buenos Ayres.<sup>2</sup> Uruguay. Southern Brazil: Rio Grande do Sul and Santa Catharina.

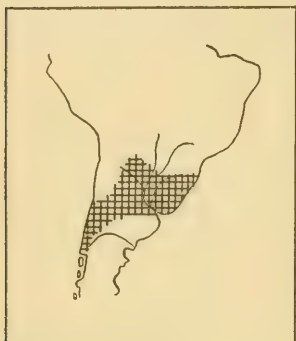


FIG. 2. Distribution of *Aeglea levis* (Latr.).

As may be seen, the extremities of the range on the Atlantic side, Sta. Catharina and Uruguay, and the southernmost locality in Chili, near Puerto Montt, are also mentioned for the genus *Parastacus*, and in fact the distribution of *Parastacus* and *Aeglea* are almost identical (see figs. 1 and 2), only *Aeglea* seems to extend a little more to the north (Jujuy). This similarity is the more striking, since in both cases the chain of the Cordilleras, which crosses the area of distribution from north to south, has absolutely no effect; both

genera are found on either side of this mountain range, and in the case of *Aeglea levis* and *Parastacus agassizi* the identical species is found east and west of the Cordilleras. This fact is very significant, and important conclusions may be derived from it.

#### C. CHOROLOGY OF THE FRESHWATER CRABS OF THE FAMILY POTAMONIDÆ (See Figures 3 and 4.)

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<sup>1</sup> Nobili, *G. Boll. Mus. Torino*, V. 11, No. 265, 1896.

<sup>2</sup> I have received from the Museum in La Plata specimens that are labeled Ensenada, Rio de la Plata.



FIG. 3. Distribution of the subfamilies *Potamoninae*, *Decapodinae* and *Potamocarcininae*.



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According to Ortmann (1897) the family of *Potamonidæ* Ortm. (= *Thelphusidæ* Dan.) is divided into four subfamilies: *Potamoninæ* Ortm., *Deckeniinæ* Ortm., *Potamocarcininæ* Ortm.,<sup>1</sup> and *Trichodactylinæ* Ortm. The first two belong to the Old World, the last two inhabit the New World.<sup>2</sup>

#### 1. Subfamily: POTAMONINÆ.

The subfamily *Potamoninæ* is in very poor condition, systematically. Not only our knowledge of the very numerous species is rather incomplete, but also their arrangement into genera and subgenera is by no means satisfactory. Generally, it seems that we can distinguish two genera: *Parathelphusa* M.-E. and *Potamon* Sav. (= *Thelphusa* Latr.), to which possibly a third one is to be added,

<sup>1</sup> = *Pseudothelphusinæ* Ortmann and Rathbun (1898, p. 508). The division into genera varies considerably with Ortmann and Rathbun respectively (see below), and the name of the subfamily depends on the classification accepted.

<sup>2</sup> According to Alcock (*Journ. Asiat. Soc. Bengal*, Vol. 69, 1900, p. 279), also *Gecarcinus* (one species in the peninsula of India), which was placed hitherto with the family *Gecarcinidæ*, belongs to the *Thelphusidæ* (= *Potamonidæ*). If this is so, we ought to create, possibly, a separate subfamily for this genus.



the very incompletely known *Erimetopus* of Rathbun. The value of a few other genera, created by various authors, is extremely doubtful.

*Parathelphusa* is represented by typical species in the northern parts of India, in Burma, Siam, Anam, Malacca, Southern China (Hongkong and Canton), and in the Sunda Islands: Sumatra, Borneo, Java, extending to Timor and New Guinea. With the same genus some other forms have been classified which are found in certain parts of Africa (Congo basin and Nile river); but these have been placed by the present writer in a subgenus (*Acanthothelphusa*) of *Potamon*, since they differ in their general shape very strikingly from the Asiatic species of *Parathelphusa*. Unfortunately these African species are very poorly known; only of the Nile species figures have been published (Milne-Edwards and Hilgendorf), and according to these it is impossible to unite this species and its supposed allies with *Parathelphusa*.<sup>1</sup>

As regards the genus *Potamon*, it is divided into several subgenera, which, however, are not very sharply defined. Aside from the doubtful subgenus *Acanthothelphusa* just mentioned, there are three of them which are generally recognized: *Potamon* (sens. strict.), *Potamonautes* Macl., and *Geothelphusa* Stps.<sup>2</sup>

The centre of the subgenus *Potamon* is, no doubt, in India and Farther India. Thence it extends eastward to the greater Sunda Islands (Sumatra and Java); it is found in the Philippine Islands, but does not advance any farther in this direction. Northward it enters China, where it is known from the Yang-tse-Kiang (see Doflein, 1902, p. 662). It does not seem to pass beyond the Himalaya Mountains to the north, but extends considerably westward (possibly in a single species), going through Persia to the Transcaspian countries, crossing the Caucasus Mountains and extending to the Crimea; from Mesopotamia it extends to Syria and Asia Minor, where it reaches the Mediterranean countries, and here it is found in Northern Egypt, Turkey, Greece, Italy, Sicily, and

<sup>1</sup> Possibly *Platythelphusa* A. M.-E. (see Hilgendorf, 1898, p. 21) from Lake Tanganyika also belongs here.

<sup>2</sup> I disregard, for the present, the subgenus *Perithelphusa* de Man (1899, p. 70), which contains apparently rather primitive forms of *Geothelphusa*, and, on account of its exclusive occurrence in Borneo, may be left united with *Geothelphusa*. As to *Platythelphusa*, see the last note. As to *Hydrothelphusa* A. M.-E., see below.

farther in Algiers as far as Oran.<sup>1</sup> It is a remarkable fact that this subgenus is entirely absent from Africa proper, *i.e.*, the part of it that lies to the south of the Sahara Desert.

The subgenus *Potamonautes*, on the contrary, has its chief centre of distribution in tropical Africa. It has been found, beginning at Liberia, all along the western coast as far as Mossamedes. It is found in the interior, in the region of the upper Zambesi (Kazungula), extends over Transvaal to the Cape Colony, and northward all along the eastern coast (Natal, Mozambique) to German East Africa. Also in the eastern part of the interior it is represented, for instance, in the headwaters of the Nile (Victoria Nyanza) and in the Somali country. From the upper Nile it extends down the Nile valley as far as Bahr-el-Gebel in the Egyptian Soudan. It is also found on the Island of Socotra and in Madagascar, although the species of the latter island do not seem to belong to the typical form of this subgenus.<sup>2</sup>

<sup>1</sup> A. Milne-Edwards reports a species that is identical with an Indian (*P. leschenaudi* (M.-E.)) from Mauritius: this locality, however, lacks confirmation. As regards the Madagassian species of *Potamon*, their systematic position is doubtful, and they possibly do not belong to this subgenus. Compare next note.

<sup>2</sup> Three species of *Potamon* are known from Madagascar. *P. goudoti* (M.-E.) (see A. Milne-Edwards, 1869, p. 172, Pl. 8, Fig. 4) is a peculiar form, but its postfrontal crest distinctly points to *Potamonautes*. A. Milne-Edwards compares it with *P. obesum* A. M.-E. from Zanzibar, and indeed it seems to be closely related to it. The latter species is also an abnormal type of *Potamonautes*, and forms with several others a group that is peculiar to East Africa; but there is no reason to separate this group from *Potamonautes*, and thus we may safely regard *P. goudoti* as a *Potamonautes*. The second species is *P. madagascariense* (A. M.-E.) (*Ann. Sci. Nat. Zool.*, Ser. 5, Vol. 15, 1872). As to this form, the diagnosis of which is very brief, and which has not been figured, its author says that it is a true *Thelphusa* (*i.e.*, subgenus *Potamon*), but this seems hardly correct according to the description of the postfrontal crest, which is said to be simply interrupted in the middle, while the median parts of it are not advanced beyond the rest. This would better agree with *Potamonautes*. The third species is regarded by A. Milne-Edwards (*Ibid.*, 1872) as the type of a separate genus, *Hydrothelphusa* (*H. agilis* A. M.-E.). This genus is said to be characterized by the flat carapace, which is scarcely dilated and almost quadrangular, and by the horizontal front. The postfrontal crest is distinct and interrupted. Since no figure is given, it is hard to form an opinion as to the relation of this form to others, but it seems to be very peculiar.

Thus it seems that the Madagassian species of *Potamon* show, in some respects, a distinct relation to East Africa and the subgenus *Potamonautes*, while in others they appear quite peculiar. (This is opposed to the opinion expressed by myself in 1901, p. 1290, footnote.)

The main range of *Potamonautes* in Africa seems to be almost continuous, but absolutely isolated from it is a secondary centre in South Asia. Here this subgenus is represented in India, and thence it extends to Farther India, and reappears on some of the islands: Pulo Condore on the coast of Cochin China, in the Philippine Islands, Celebes and New Guinea. These latter localities are distinctly discontinuous.

The third subgenus, *Geothelphusa*, undoubtedly has its centre in the extreme East, and it is most characteristic for the Malaysian Islands. On the Asiatic continent it seems to be absent; but it is found abundantly in Sumatra, Java, Borneo, and extends eastward over Aru Island and New Guinea to North Australia, where it is found on the Cape York Peninsula, and in Queensland as far as Port Mackay.<sup>1</sup> Northward this subgenus ranges over the Philippine and Loo-Choo Islands to Japan, where it reaches its northernmost station in the neighborhood of Tokyo.

On the continent of Asia typical species of this subgenus have not been found; indeed a few small species from India have been described which might be united with this subgenus, but this is by no means sure.

But this identical subgenus, *Geothelphusa*, is apparently found in another locality isolated from the rest of the range: this is *P. berardi* (Aud.) from Egypt (Nile river). This species, however, is also morphologically isolated from the rest; and further, this subgenus is recorded by Rathbun from Liberia (*P. macropus* Rthb., 1898), and some species from East and Central Africa, related to *P. obesum*, mentioned above, resemble, in the reduction of the postfrontal crest, the subgenus *Geothelphusa*,<sup>2</sup> while on the other hand they are undoubtedly related to the subgenus *Potamonautes*. It is quite possible also that *P. berardi* from Egypt (Kairo southward to Mount Elgon) belongs to this East African group. In my opinion, all these species do not properly belong to *Geothelphusa*, and we have to deal here again with a case of convergency: the

<sup>1</sup> According to de Man, an Australian species (*P. transversum* (Mrts.)) is also found in the Fiji Islands; but this lacks confirmation.

<sup>2</sup> These are *P. obesum* (A. M.-E.), Zanzibar; *P. emini* Hlgdf., *P. newmanni* Hlgdf., *P. pilosum* Hlgdf. (Hilgendorf, 1898), all three from East Africa and the region of the Great Lakes. Possibly *P. socotrense* Hilgendorf (1883, *Zeitschr. d. Naturw.*, Ser. 4, Vol. 2) = *P. granosum* Koelbel (*SB. Akad. Wien*, Vol. 90, 1885) belongs here.



tendency to reduce the postfrontal crest has developed in the East African forms independently from the typical *Geothelphusa*, and the East African (possibly also the Liberian) species form a peculiar branch of *Potamonantes*.

The genus *Erimetopus* of Rathbun is found so far only in the Congo basin.

Considering the distribution of the subfamily *Potamoninae* in general, we see that it is continuous over the whole of tropical Africa, then it extends through the Nile valley into the Mediterranean regions and connects with the Asiatic range, which goes from Syria over Mesopotamia, Persia to India, China and the Malaysian archipelago, over which it finally reaches Northern Australia and Japan. This whole range is practically continuous, only the larger continental islands (disregarding the smaller ones), Madagascar and the Sunda Islands, the Philippines, New Guinea and Japan, constituting breaks in the continuity.

Within this large area, however, we are able to distinguish two main divisions: an African, characterized by the prevalence of the subgenus *Potamonantes*, the complete lack of the subgenus *Potamon* (and possibly of *Geothelphusa*), and an Asiatic-Australian division, characterized by the prevalence of the subgenus *Potamon*, the presence of *Geothelphusa* (in its eastern part), and the scarcity of *Potamonantes*. Both divisions are practically connected by the Nile valley; this connection, however, does not seem to represent the original condition, but suggests a secondary one, since different types are here associated which are not at all related to each other. Species of *Potamonantes*, to which subgenus, according to our opinion, *P. berardi* also belongs, migrating northward from the Soudan, have met here in Lower Egypt a species of the subgenus *Potamon* (*P. fluviatile*), which had migrated westward from India. Both subgenera entered the Nile valley from different directions and accidentally became occupants of the same territory, but the Nile valley is not the route of migration by which African species migrated into Asia or *vice versa*.

Aside from this narrow connection, the fauna of freshwater crabs of tropical Africa is very sharply characterized and isolated from Asia,<sup>1</sup> and the fact is worth special mention that North Africa

<sup>1</sup> The peculiarity of the African fauna is emphasized by the doubtful forms of *Parathelphusa* (or *Acanthothelphusa*), and by *Erimetopus*.

(Lower Egypt and Algiers) points, like the whole of the Mediterranean region, to India, from which locality the species present there, *P. fluviatile* (Latr.), has apparently migrated in an east-westerly direction over Persia, Mesopotamia and Syria. *P. fluviatile* has been actually recorded from western India; at any rate the most closely allied species to this one are found in India and China.

Other remarkable facts in the distribution of this subfamily may be summed up thus:

1. The Asiatic as well as the African part of the range is occupied by the subgenus *Potamonantes*. It is impossible to say which was the original home of *Potamonantes*, but this much is evident, that it must have been present in both parts at a comparatively early time, it being probably older than *Potamon* sens. strict. In Africa *Potamonantes* attained its highest development, being the prevailing type there and showing great variety.

2. Madagascar, while belonging distinctly to Africa in its fauna, possesses some rather peculiar types.

3. The subgenus *Potamon* originated in Asia, apparently at a time when there was no connection any more with tropical Africa or Madagascar. The immigration of *Potamon* into the Mediterranean countries, across Persia, etc., is probably a comparatively recent one, since the route of immigration is easily traced and occupied by one single species.

4. The Malaysian and Philippine Islands, Japan and North Australia possess in *Geothelphusa* a very peculiar group. This distribution of *Geothelphusa* does not correspond to that of *Parathelphusa*, *Potamonantes* and *Potamon* sens. strict., which are also found in the Malaysian Islands. *Potamonantes* and *Parathelphusa* are similar in this respect, possessing on the Sunda Islands only scattered stations (as far as New Guinea), which by their discontinuity express an ancient condition. *Potamon* points directly to an Indian origin, extending only to Sumatra, Java and the Philippines, but going not any farther to the east.

5. The position of *Parathelphusa* is hard to understand. If it is really absent in Africa, as we believe, its distribution in Asia is rather eastern than western, being chiefly found in Farther India. Its extension over the Sunda Islands to New Guinea points to old conditions. Since the morphological relations of *Parathelphusa* to the rest of the subfamily are not well understood, it is better to exclude it from our further consideration.

Supposing that this subfamily must have had once a more or less continuous distribution, we are to draw from this the following conclusions as to the geographic conditions of the past :

1. *Africa and India must have been connected once. This connection, however, was not by way of North Africa, Arabia and Persia, and is possibly identical with that from Africa over Madagascar to India, discussed above* (see No. 5, p. 295).

2. *Madagascar must once have been a part of Africa.*

3. *The Indo-Malaysian Islands, including the Philippine Islands, Loo-Choo Islands and Japan, must have been once connected not only between themselves, but also with New Guinea and North Australia (as indicated by *Geothelphusa*). On the other hand, the distribution of the typical forms of *Potamon* indicates that some of these islands (Sumatra, Java, Philippines) were once connected with the continent of Asia. Then, again, by *Potamonautes* (and *Parathelphusa*) the former continuity of the whole region from India to New Guinea is indicated* (see p. 295). *It is evident that here repeated and important changes of the mutual connections have taken place at different periods of the past.*

The history of the subfamily of *Potamoninæ* would then be this: Its centre lies in an Afro-Indian continental mass, which was divided subsequently into two parts, tropical Africa and India. From India the subfamily extended at a very early period over the Sunda Islands, Philippine Islands, which consequently must have formed a part of the continent, and this continental connection extended as far as New Guinea and Australia, but not without repeated interruptions and changes. In the region of instability and change lies the home of the subgenus *Geothelphusa*, which was able at a certain time to go as far north as Japan. A separate branch of the subgenus *Potamon* was sent out from India westward, which finally reached the Mediterranean countries, where it met in the lower Nile valley a branch of the African subgenus *Potamonautes* which came down the Nile from the south.

## 2. Subfamily: *Deckeniinæ*.

The second subfamily of the Old World, the *Deckeniinæ*, contains only one genus, *Deckenia* Hlgdf. (see Ortmann, 1897, p. 314), of which three species have been described :

*D. imitatrix* Hlgdf. Interior of British East Africa: Taro (Hil-



gendorf, 1898, p. 23) and Somali country (de Man, 1898, p. 270).

*D. mitis* Hlgdf. (1898, p. 24). German East Africa and British East Africa (Mombas).

*D. alluaudi* A. M.-E. and Bouv. (= *cristata* Rthb.). Seychelle Islands.

The *Deckeniinae* are, as is expressed by their morphological characters (Ortmann, 1897, p. 297), a highly specialized group of the family which may be connected without hesitation with the genus *Potamon*, and possibly with the African branch of it. This subfamily is a group localized in East Africa, and the presence of one of the species in the Seychelles indicates a former connection of these islands with East Africa. It is quite probable that this connection is an additional proof for that old Afro-Indian landbridge discussed above, which included Madagascar (see No. 5, p. 295, and No. 1, p. 305).

### 3. Subfamily: *Potamocarcininae*.

The subfamily *Potamocarcininae* (= *Pseudothelphusinae*) is restricted to America and is wanting in the Old World. The systematic arrangement of it is a matter of discussion, since the two revisions published by Rathbun and Ortmann do not agree as to the principles of division.

Regarding the subfamily as a whole, its range comprises the following parts: West Indies—Greater Antilles: Cuba (including the Isle of Pines), Hayti, Porto Rico (including Santa Cruz); Lesser Antilles: Guadeloupe, Dominica, Martinique, Sta. Lucia. On the continent its range begins in Mexico; the northern boundary is marked by a line beginning in Tepic Territory, running through the States Jalisco and Guanajuato to Vera Cruz. Thence the range covers the southern parts of Mexico, Guatemala, Nicaragua, Costa Rica and Colombia, and extends eastward over Venezuela (including Trinidad) and Guyana. In a southerly direction it passes from Colombia into Ecuador, Peru and to Northern Bolivia. In the latter region it is found in the Cordilleras and the tributaries of the upper Amazonas river. An isolated locality is Pará, on the southern side of the mouth of the Amazonas river (*Pseudothelphusa agassizi* Rthb.).

In order to get an idea of the distribution of the different genera

of this subfamily, it is necessary to discuss the systematics of it. Ortmann distinguishes four genera: *Potamocarcinus*, *Epilobocera*, *Hypolobocera* and *Kingsleya*, while Rathbun accepts the following: *Epilobocera*, *Potamocarcinus*, *Pseudothelphusa* and *Rathbunia*. Generally, Ortmann's *Potamocarcinus* corresponds to the genera *Potamocarcinus* and *Pseudothelphusa* of Rathbun, and the close affinity of these two is also admitted by Rathbun, so that their union (under *Potamocarcinus*) is well supported. But in this case, we are to exclude from *Potamocarcinus* the species *sinuatifrons* Kgs. (and Ortm., nec A. M.-E.) = *haytensis* Rathb., which belongs to *Epilobocera*. If we add this latter species to Ortmann's *Epilobocera*, this genus corresponds exactly to *Epilobocera* Rathbun. *Hypolobocera* of Ortmann is classed by Rathbun with *Pseudothelphusa* (*Potamocarcinus* of Ortmann), and rightly so, as we now believe. *Kingsleya* Ortmann is put by Rathbun with *Potamocarcinus* (sens. strict.); this, however, does not seem to be justified, since then the very peculiar shape of the orbita is neglected. While in all other forms of the subfamily the lower orbital margin possesses on the inner end a suborbital lobe, which may unite with the front, in *Kingsleya* the lower orbital margin itself joins the front, while the suborbital lobe is hidden. This character, connected with the extremely reduced condition of the exopodite of the third maxilliped, which also does not find its like in the whole subfamily, fully warrant, in our opinion, the creation of a separate genus. The genus *Rathbunia* of Nobili is founded upon a single species, and its chief character is taken from the shape of the meropodite of the third maxilliped, which is narrower than usual at the proximal end. In all other respects this genus agrees absolutely with *Pseudothelphusa* (resp. *Potamocarcinus* of Ortmann), and a generic separation does not seem to be necessary.

As a compromise between both generic divisions I should like to suggest the following:

Genus: *Epilobocera* Stps. (corresponding fully to *Epilobocera* Rathbun).

Genus: *Potamocarcinus* M.-E. (= *Potamocarcinus* Ortm. (excluding *sinuatifrons* Ortm. = *haytensis* Rathb.) + *Hypolobocera* Ortm.).

1. Subgen. *Potamocarcinus* M.-E. (genus, according to Rathbun, excluding the species *latifrons* Rand.).

2. Subgen. *Pseudothelphusa* Sauss. (= genus *Pseudothelphusa* Rathb.).

3. Subgen. *Rathbunia* Nobili (= genus Nobili and Rathb.).  
Genus *Kingsleya* Ortm.

It is entirely a matter of taste whether one prefers to regard *Potamocarcinus*, *Pseudothelphusa* and *Rathbunia* as genera or subgenera. This much, however, is evident, that they are much more closely allied to each other morphologically than to either *Epilobocera* or *Kingsleya*. Judging from the third maxillipeds (which furnish a good criterion in this respect), *Epilobocera* should be regarded as the most primitive form, *Potamocarcinus* (in the largest sense) would be typical and *Kingsleya* the most specialized.

This division into three genera corresponds well to the geographical distribution of the different forms (see Rathbun, 1898, pp. 532-537).

*Epilobocera* contains six species which are restricted to the Greater Antilles: Cuba, Isle of Pines, Hayti, Porto Rico and Santa Cruz Island.

*Potamocarcinus* (in the widest sense) contains 47 species<sup>1</sup>, which cover the whole continental range of the subfamily from Mexico to Bolivia and Pará, the Lesser Antilles and of the Greater Antilles, Cuba and Hayti. The subgenus *Pseudothelphusa* has the same range, while of the two species of *Potamocarcinus* (sens. strict.) one is found in Guyana, the other in Costa Rica. *Rathbunia* is known only from Darien. *Kingsleya* is so far known only from Guyana.

The range of the subfamily on the continent seems to be perfectly continuous; only *P. agassizi* from near Pará appears to be more or less isolated. The most closely allied forms to this one (*reflexifrons* Ortm. and *denticulatus* M.-E.) are found in the region of the upper Amazonas and in Guyana respectively, so that this locality (Pará) is possibly connected with Guyana. There is, however, the other possibility, that along the course of the Amazonas river a connection exists between its lower part (Pará) and its upper (upper Amazonas). A very important fact is that Pará is

<sup>1</sup> Forty-two species mentioned by Rathbun, one described subsequently by Doflein (1900, *P. principessa*, Colombia), one described by Nobili (1901, *P. caputii*, Ecuador); these forty-four belong to *Pseudothelphusa*. Two species belong to *Potamocarcinus* and one to *Rathbunia*.



the only locality known for this subfamily to the south of the Amazonas river, at least in Brazil. Generally, we may call this river the southern boundary of the range of the subfamily, although in the Cordilleras of Peru and Bolivia *Potamocarcininae* are found more to the south.

The localities of this subfamily in the West Indian islands are now separated from the main range on the continent. Here we can distinguish two groups: the Greater Antilles possess as a characteristic type the genus *Epilobocera*, which is found nowhere else. At the same time we have in Cuba three species of *Pseudothelphusa*, of which one (*americana*) is also found in Hayti. This same species, *P. americana* Sauss., is found largely distributed in Mexico (States of Guanajuato, Morelos, Puebla, Guerrero, Oaxaca), and, further, another Cuban species (*terrestris* Rthb.) has also been reported from Mexico (Jalisco and Tepic), while the third species (*affinis* Rthb.) is restricted to Cuba.<sup>1</sup>

The second group within the West Indies is formed by the islands of Gaudeloupe, Dominica, Martinique, St. Lucia, where one species (*P. dentata* (M.-E.)) is found. According to Rathbun (1898, p. 524), the most closely allied forms to this are *P. garmani* Rthb. from Trinidad and Venezuela, and *P. fossor* Rthb. from Venezuela.

The above chorological and systematic facts justify the following conclusions:

1. *The distribution of the Potamocarcininae in Central and South America is remarkable, in so far as it does not go southward beyond the Amazonas river.*

2. *The West Indian islands must have been once connected with Central and South America. The freshwater crabs of the Greater Antilles point to a connection with Mexico, as well as to a connection between themselves, after they were separated from the mainland (Epilobocera). The freshwater crabs of the Lesser Antilles point to a connection with Trinidad and Venezuela.*

#### *Connection of the Potamocarcininae and Potamoninae.*

As is accepted by all authors, the affinity of the *Potamocarcininae* of the New World with the *Potamoninae* of the Old World is beyond question, and this affinity is expressed by their position as

<sup>1</sup> This locality, given for a specimen from the old collection of Guérin in Philadelphia, needs confirmation.

two subfamilies within the same family, *Potamonidæ*, which has never been disputed.<sup>1</sup> Consequently the idea suggests itself that both subfamilies have a common origin, or have descended the one from the other. Transitional forms between them are not known; this, however, is not astonishing if we consider their geographic isolation.

The present writer has called attention to the presence in Central Africa of a group of *Potamon*, which he has designated as the subgenus *Acanthothelphusa*. These species have been united by others with *Parathelphusa*, which classification we do not consider to be correct. Although these species are very poorly known, it seems impossible to unite the type-species of *Acanthothelphusa* (from the Nile) with *Parathelphusa*, and it would be well to examine the other species more closely with a view to their possible relation to the American *Potamocarcininae*.

Whether this prove to be so or not, this much is unquestionable, that the West African *Potamoninae* are geographically most closely approached by the South American *Potamocarcininae*, and thus a former connection of the respective parts, West Africa and northern South America, is suggested (see Ortmann, 1901, p. 1291).

#### 4. Subfamily: *Trichodactylinae*. (See Fig. 4.)

Finally, we are to consider the subfamily *Trichodactylinae* Ortm., which is divided, according to Ortmann (1897, p. 298), into two genera, *Trichodactylus* Latr. and *Orthostoma* Rand., which latter generic name, however, is to be abandoned as preoccupied. Its place is to be taken by *Sylviocarcinus* or *Dilocarcinus* M.-E., 1853. But even *Trichodactylus* and *Dilocarcinus* (in its largest sense including *Sylviocarcinus*, according to Ortmann, and being identical with *Orthostoma*) are not always sharply defined, and, further, the

<sup>1</sup> According to Ortmann (*Zool. Jahrb. Syst.*, Vol. vii, 1893, p. 430), the *Thelphusidæ* (*Potamonidæ*) are possibly derived from *Menippidæ*—i.e., primitive *Xanthidæ* (in Alcock's sense). They are primitive *Cyclometopa*, which, however, in certain characteristics, probably connected with their habits, are more highly and abnormally developed, and exhibit (due to convergency?) similarities to the *Catometopa*.

Alcock (*Jour. Asiat. Soc. Bengal*, V. lviii, Part 2, No. 1, 1899, p. 3) is inclined to regard the *Thelphusidæ* as descendants of the *Oziinae* or *Eriphiinae* (higher *Xanthidæ*), and takes them for very highly specialized *Cyclometopa*.

Both views agree in that the family *Xanthiida* is supposed to be the ancestral stock of these freshwater crabs.

distinction of species seems to be very arbitrary within these genera. Up to the present, about five or six species of *Trichodactylus* and about fourteen species of *Dilocarcinus* have been described. In the following we shall discuss them all together.

The subfamily covers an area that comprises the larger southern half of Brazil (Bahia, Rio de Janeiro, Goyaz, Minas Geraës, S. Paulo, Sta. Catharina, Rio Grande do Sul). It is found in Paraguay, and in the Argentinian provinces: Misiones, Chaco and near La Plata (Ensenada).<sup>1</sup> Further, species of *Trichodactylinae* are very abundant in the Cordilleras, in the region of the headwaters of the Amazonas river, namely, in Bolivia (province Beni, Yocuma river, belonging to the upper Madeira), in Peru (rivers Ucayali, Huallaga), and in the Marañon at Nauta and Loreto (Ecuador). Since there are also representatives known from the lower Amazonas (Island Marajo), all these localities named seem to form a continuous area, which extends from the Amazonas river southward to La Plata, and from the Atlantic Ocean westward over Brazil, Paraguay and Argentina to Bolivia and Peru, where it reaches the eastern slopes of the Cordilleras. Apparently isolated from this area, several species are found in Guyana, and, finally, one species (*Trichodactylus quinquedentatus* Rthb.) is known from the upper parts of the river Magdalena in Colombia, and from the Escondido river in Nicaragua.

It is quite possible that the isolated stations in Guyana, Colombia and Nicaragua will be connected by subsequent discoveries (Colombia is very near to the localities of the upper Amazonas), and then we would have for this subfamily a continuous range, which comprises the whole of South America southward to La Plata, and from the Atlantic Ocean to the eastern slopes of the Cordilleras, and which extends in Central America as far as



FIG. 4. Distribution of the Crabs of the subfamily *Trichodactylinae*.

<sup>1</sup> I have received from the La Plata Museum specimens of *Dilocarcinus panoplus* (Mrts.) from Ensenada.

Nicaragua. It is to be remarked that none of the localities is situated in the drainage of the Pacific Ocean, but all are in that of the Atlantic.<sup>1</sup>

This distribution does not offer any remarkable facts. The *Trichodactylinae* seem to belong to the tropical parts of the Atlantic slope of South America, and their centre is somewhere in Brazil; from Brazil they extend in every direction until, in the east the Atlantic Ocean, in the west the Cordilleras, in the south the climate of Argentina form barriers. To the north the most advanced station is in Nicaragua; here no natural boundary (climatic or topographic) is marked.

Further speculations as to the distribution of this subfamily do not seem to be very promising until we are better acquainted with the chorological facts. The whole appearance presented by the distribution is a recent one; probably it is continuous and, in most directions, limited by natural boundaries. In this respect it is strikingly distinguished from the other groups of the family *Potamonidae* discussed above.

I have the impression that the *Trichodactylinae* are not so closely connected, systematically, with the other subfamilies of the *Potamonidae* as was believed hitherto. In fact, transitional forms to any of the other subfamilies are not known, and the *Trichodactylinae* are morphologically isolated and sharply defined. Moreover, the whole "habitus" of these crabs is so entirely different from that of the *Potamocarcininae* that it is worth while to revise the systematic relations of these groups. As I venture to imagine, it will be found, possibly, that the *Trichodactylinae* form a group that is much more sharply isolated, systematically, and that has little to do with the family *Potamonidae*. This much is evident: according to its morphologic isolation, we ought to expect that the *Trichodactylinae* are a comparatively ancient group; but this is contradicted by their distribution, which possesses a remarkably recent character.

These are the reasons why we shall exclude the *Trichodactylinae* from our further discussions.

<sup>1</sup> This is contrary to what we have in the *Potamocarcininae*, which are found also on the Pacific slope in Ecuador, and especially in Central America and Mexico.



## PART II. RECONSTRUCTION OF ANCIENT GEOGRAPHIC CONDITIONS.

BIBLIOGRAPHY.<sup>1</sup>(a) *Papers Written from a Zoogeographical Standpoint.*

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- "The Theories of the Origin of the Antarctic Faunas and Floras" (*Amer. Natural.*, Vol. xxxv, 1901, pp. 139-142).
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- OSBORN, H. F. "The Geological and Faunal Relations of Europe and America during the Tertiary Period and the Theory of the Successive Invasions of an African Fauna" (*Science*, April 18, 1900, pp. 561-574; see also *Ann. N. Y. Acad. Sci.*, Vol. xiii, 1900, pp. 1-72).
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(b) *Papers of a Geological Character.*

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- HILL, R. T. "The Cretaceous Formations of Mexico and their Relations to

<sup>1</sup> Only the more important papers are given in the following list. Others, quoted only incidentally, shall find their place in footnotes.

<sup>2</sup> I quote only the following two papers of von Ihering, although he has published several more on these and kindred subjects. But these two contain the essence of his theories.

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In the following we shall endeavor to answer the questions: *What connections are suggested by the distribution of the freshwater Decapods, and Is there any other evidence, in the first place, of a geological character to support them?* The solution of these questions will furnish us the key for the reconstruction of the old geographic conditions.

If we recall the connections suggested by the distribution of the freshwater Crustaceans, we can collect them in the following list:

1. *Connection of northeast Asia with northwest America across Bering Sea* (see pp. 290, 291, 295).
2. *Connection of east Asia with Australia* (see pp. 295, 305).
3. *Connection of south Asia with Madagascar and Africa* (see pp. 295, 305, 306).
4. *Connection of New Zealand with Australia* (see p. 295).
5. *Connection of Australia (resp. New Zealand) with South America* (see p. 295).
6. *Connection of the West Indies with Central, resp. South America* (see pp. 295, 309).
7. *Connection of South America with Africa* (see p. 310).

Other important questions arose out of the distributional facts, which may be classified under the following heads:

8. *General relations of North, Central and South America* (see pp. 295, 309).
9. *Relations of Africa to the rest of the world* (see pp. 303, 304).
10. *Relations of Europe to Asia (and Africa)* (see pp. 291, 295, 304).

We shall take up these different items in the order here indi-

cated. But before we do so, we have to say a few words by way of explanation and introduction, characterizing the value of the study of the freshwater Decapods for these purposes.

In all the following discussions, the fundamental supposition has been made that freshwater crayfishes, as well as freshwater crabs, do not possess any exceptional means of dispersal; that is to say, that they are restricted to fresh water and cannot exist in salt water; that they cannot leave the water for any continued period, and consequently cannot migrate over land to any extent; and, finally, that they do not possess in any stage of their life, and especially not in the egg or larval stage, any means or devices which permit their passive transport. We may specify these three points in the following way:

1. The restriction to fresh water is not absolute. There are a few exceptions, namely:

*Potamobius pachypus* (Rthk.) is found in the Black and Caspian Seas in brackish and salt water.

*Potamobius trowbridgei* (Stps.) has once been collected in salt water at Monterey, California (Faxon, 1898, p. 666).

*Cambarus uhleri* Fax. is characteristic for the marshes of the coast of Maryland, and lives in fresh, brackish, and salt water.

*Cambarus montezumæ* Sauss. has been found, in one case, in a salt lake in Mexico (Lake Tezcoco, near City of Mexico; see Faxon, 1885, p. 123).

*Potamon fluviatile* var. *ibericum* (Bisb.) is found in fresh water and salt water of the Caspian Sea (see Ortmann, 1897, p. 302).

On account of the small number of these cases, we have to regard them as exceptional, and they are, no doubt, secondary adaptations. In fact, none of these species is a true saltwater form, they being always more or less euryhalin, and frequenting also brackish or freshwater. Thus we may say, generally, *that both, crayfishes and crabs, discussed here, are true freshwater animals, and preëminently so, and that a migration across oceans or parts of oceans is practically excluded.*

2. Being animals breathing by gills, crayfishes and freshwater crabs cannot leave the water. This rule is without exception with the *Potamobiidæ* and *Parastacidæ*; they may leave the water for a short time, but a prolonged stay outside of it is always fatal. There are only a few species in North and South America, and in Aus-

tralia, burrowing in mud, which leave the water habitually; but they always have to return to the water to moisten their gills, and their burrows end in water. The forms most adapted to a subterranean life are probably the two species of *Engæus* in Tasmania. In general, *for the crayfishes, tracts of land without water (deserts) are absolute barriers.*

The *Potamobiidæ* lead a rather amphibic life and leave the water, in many cases, habitually. Yet they always depend on the presence of water and cannot go far out of easy reach of it. Some of the species (*Potamon fluviatile* in Persia, etc.) live in steppes, where there is a scarcity of water, but here they always are found near some kind of water supply. In general, *they also cannot exist in deserts.*

3. As in all other Decapods, also in crayfishes and freshwater crabs the eggs are carried and hatched under the abdomen of the female. There is, as far as we know, no free metamorphosis of the young (known in *Potamobius*, *Cambarus*, *Potamon*), and the young hatch in a stage similar to the parents. Thus there seems to be no means which effect, under normal conditions, an increased facility of dispersal in an active or passive way among the young ones. There may be, occasionally, a passive transport by other animals (water fowl), but such cases can only be exceptions and have never been observed. The whole character of the distribution of the different species is *against the assumption of exceptional means of dispersal.*

#### I. CONNECTION OF NORTHEAST ASIA WITH NORTHWEST AMERICA BY WAY OF BERING SEA.

A connection of northeast Asia with northwest America is postulated, as we have seen above, by the presence of *Potamobiidæ* in the region of the Amur river, Korea, and north Japan on the one side, and in western North America on the other; the direction of this connection is indicated by the presence of *Potamobius nigrescens* (Stps.) in Unalaska.

This connection is mentioned by Jacobi (1900) under his "regions of dispersal" ("Ausbreitungsgebiete"), and is called by the name of "Berings-Strassen-Ausbreitungsgebiet." This is well known among zoogeographers. In fact, for an explanation of the very peculiar conditions of distribution of many animals of the northern hemisphere, a former connection of the northern land



masses of the Old and New Worlds is absolutely necessary, and the similarity of the land faunas of both parts, which is not explained by the present conditions, is so strong that these regions (northern Eurasia and North America) have been united by certain authors into *one* zoogeographical region, the Holarctic. As to the location of this connection, two ways are possible: either from Siberia to Alaska, or from Labrador over Greenland to Scandinavia. The latter connection, which has been discussed, from a geological standpoint, chiefly by Suess and Neumayr (for older times, Mesozoic and Tertiary), and, from a zoogeographical view by Scharff (for the Pleistocene), may be disregarded for our present purpose; there is no indication for its existence among the crayfishes. But the latter support strongly, as has been said, the other connection over Bering Strait.

Viewed from the tectonic side, this connection is quite possible. The old rocks of northeast Asia are continued into northeastern Siberia (east of the rivers Lena and Aldan) to the river Kolyma,<sup>1</sup> and farther, toward the Arctic Ocean and Bering Sea, and similar rocks are found in Alaska; and further, the chain of the Aleutian Islands is, according to Suess, another proof for the tectonic unity of the lands east and west of Bering Sea.

As regards the time of existence of this land bridge, we have to assume it during almost the whole of the Tertiary period. Osborn (1900) takes its existence for granted and demonstrates (p. 568) that during Eocene, Miocene and upward to the Pliocene, a regular exchange of the faunas of Eurasia and North America took place. In the older Pleistocene (p. 571) this connection still existed, but was interrupted in the middle Pleistocene (p. 572).

If we put the question, whether and how far this land bridge goes back in Pretertiary times, we have to consult first Neumayr's opinion as to the distribution of the Jurassic oceans and continents (1890, map, p. 336). It is true, in Siberia, deposits of Lower Jurassic age are not known, and possibly Siberia was land during this time<sup>2</sup>. There are found here, however, deposits belonging to

<sup>1</sup> See Tscherski, *Sap. Akad. St. Petersb.*, Vol. 73, Append. 5, 1893 (Russian); Review in *N. Jahrb. Mineral.*, etc., 1896, Vol. 2, p. 318.

<sup>2</sup> Land and freshwater deposits of Jurassic age are largely distributed in Siberia as coal-bearing strata. Compare the geological investigations connected with the great Siberian railroad, by Obrutchew, Gerassimow, Gedroiz, Jaworowsky. Reviews in *N. Jahrb. Mineral.*, 1899, Vol. 2, p. 111-116.

the Upper Jurassic (Neumayr, 1890, p. 329), which reach the Pacific Ocean. Beds of the same age are known on the Aleutian Islands and in Alaska. These deposits exhibit a peculiar character, which has been called the boreal or arctic type, and in this respect the Jurassic beds of the western coast of North America are very important, since they agree with the boreal type. Neumayr concluded from this that the Upper Jurassic Polar Sea sent an extension southward along the western coast of North America into the North Pacific, and its fauna also extends in this direction; by this extension of the Polar Sea, east Asia was separated from North America. Consequently there was no land bridge.<sup>1</sup>

These conditions of Upper Jurassic times continued, according to Neumayr, into the Lower Cretaceous; the Wolga-stage, with its characteristic Aucella-beds, belongs in part to the Lower Cretaceous, and the Polar basin was also in the beginning of the Cretaceous in open communication with the northern Pacific. This is represented in Koken's map (1893, pl. 1), although Asia and North America approach each other considerably. This same map, however, expresses, for the Upper Cretaceous, a separation of the Polar Sea from the Pacific, and this land connection between Asia and North America is preserved in Koken's map for the older Tertiary (*l. c.*, pl. 2). The evidence for this disconnection of the oceans in the Upper Cretaceous time is given by Neumayr (1890, p. 389-391); palæontologically, we can trace a continuous Upper Cretaceous ocean, including the northern Pacific from California to Japan, which was connected with south India. This province differs strikingly from the American-European (Atlantic) province; the Polar Sea was much reduced in size, and, to all appearances, Siberia was largely dry land and was connected with North America.

Thus there is some evidence of the existence of a land connection between Siberia and Alaska, beginning at about the middle of the Cretaceous period, and continuing up to the end of the Tertiary. Whether this connection was continuous in time, or interrupted at certain periods, is hard to decide; at all events, it was of such a character that an easy and free communication was possible between the respective parts, and this is expressed very distinctly in the faunas of the northern land masses, although the

<sup>1</sup> This Jurassic ocean forms apparently the continuation of the old Triassic basin, comprising the Pacific and Arctic Oceans (see Neumayr, p. 266).

geological evidence is very slender on account of our defective knowledge of the Beringian countries.

For our present purposes, this has the following meaning. The *Potamobiidæ* of eastern Asia, the remnants of which are known as the subgenus *Cambaroides*, had easy access to northwestern America by way of the Beringian connection, from the beginning of the Upper Cretaceous to the end of the Tertiary. Since *Cambaroides* is to be taken, as we have seen above (p. 288), for the more primitive group, the migration must have been in an easterly direction. It cannot have taken place in recent times, since this way is now rendered impossible, and just this recent (or Pleistocene) interruption (probably connected with a change of climate) has separated the Asiatic and American range of *Potamobius*. Before the middle of the Cretaceous it was also impossible for the crayfishes to pass along this line, since then this connection was not yet formed, and thus we obtain a very important lower limit for this process in the dispersal of the *Potamobiidæ* about the *middle of the Cretaceous period*. Consequently, the *Potamobiidæ* may go back, in their geological history, at least as far as this time. We shall see later that we are able to define also an upper limit for the time of immigration into North America.

## 2. CONNECTION OF EASTERN ASIA AND AUSTRALIA.

Another geographic postulate of the distribution of the *Potamobiidæ* and *Parastacidæ* is the connection of east Asia, the region of *Cambaroides*, with Australia, the main region of the family *Parastacidæ*. This same connection, from Farther India and south China over the east Asiatic islands to north Australia, is suggested by the distribution of the subfamily of the *Potamoninæ*.

Other zoogeographical facts point the same way. Pilsbry (1894, p. xlv) says that eastern Asia and China, southward to Australia, constitutes a great division in *Helix* distribution, and many other writers have emphasized the close affinity of the fauna of Australia to that of southeastern Asia, although this is true only for certain groups of animals. The opposite opinion, which generally prevails, that Australia is sharply isolated from the rest of the world in its faunal relations, is founded chiefly on the highest forms of life, the Mammals. Other groups of animals, which permit us to draw conclusions in this respect, indicate clearly that a large part of the

Australian fauna is derived from Asia (see von Ihering, 1894, p. 406, and Hedley, 1899).

This connection between east Asia and Australia (Sino-Australian) is not well expressed in Jacobi's scheme. The apparent reason for this is that Jacobi considered chiefly those groups of animals (Mammals, Birds) which do not bear upon this question. Nevertheless, some of his "regions of dispersal" come under this head, namely, the ninth, tenth, eleventh and twelfth (Papuan, Farther Indian, Philippine, southern Japanese; see Jacobi, 1900, pp. 208-210), and discussing the Papuan, he directly mentions the Oriental origin of certain elements of it, thus indicating its relation to southeastern Asia.

Studying the tectonic configuration of the repective parts, we are to remember that Australia belongs to the old, Palæozoic Gondwana land of Suess (1888, p. 317 ff.), which also comprised Africa and India. But we cannot refer to this old connection of Australia with India, since India in turn was not then united with the rest of Asia, and since this connection was destroyed in very early times, possibly in Palæozoic. For a tectonic connection of Australia and eastern Asia (excluding India) we have only evidence to the contrary.

On the other side, the eastern parts of present Asia, especially China, northeastern Siberia, and Farther India, form a more or less complete tectonic unit. Suess (1888, pp. 206-242) has shown that this whole region consists largely of old archaic and palæozoic rocks, which form, in northern China, an old continental mass, in the south a series of folded mountain ranges (p. 287), which continue into the mountains of Tonkin and Anam as far as the mouth of the river Mekong. In this whole region no Mesozoic deposits (with the exception of Rhætic beds in Tonkin) are known. According to Koken,<sup>1</sup> a Triassic ocean extended from the region of the Himalaya mountains and Central Asia to the shores of the present Pacific, covering a large part of China. The latter may have been land before Rhætic times; but at present we have only evidence that it was surely land in the Jurassic period.<sup>2</sup>

<sup>1</sup> *Neues Jahrb. f. Mineral.*, etc., 1900, Vol. 1, p. 196.

<sup>2</sup> See Loczy, L. von, *Wissenschaftliche Ergebnisse der Reise des Grafen Bela Szechenyi in Ostasien*, Vol. 3, 1899; the Central-Chinese sea (south of the Kuen-Lun mountains) disappeared at the end of Triassic and in Jurassic times.



Thus it is clear that we may assume the existence of this continent, the Sinic, from the Jurassic upward.

Further, according to Suess, the chains of islands accompanying this old continent on its southern and eastern sides are tectonically connected with the latter. One of them is formed by the mountain ranges which form the Japanese and Philippine Islands, consisting of old rocks, and, in the south, we can trace a similar chain (Suess, 1885, pp. 579-588), which begins with the Burmese ranges, and extends over Malakka, Sumatra, Java eastward, possibly as far as New Guinea.

Thus, nothing in the tectonic configuration is opposed to the theory that at least a large part of the Indo-Malaysian islands belongs to the continent. But this does not give us any proof for an actual former connection of these islands with the Sinic continent. This can only be decided by geological investigation of the respective parts. Unfortunately, our knowledge in this respect is very scanty.

Neumayr (1890) constructs in his map, mentioned above, an old Jurassic continent, the *Sino-Australian*, which, with reference to eastern Asia, is well supported, and the Australian part of which is also established by the fact that large parts of Australia possess a very old age (Gondwana land). The connection of both goes over the present Indo-Malaysian Archipelago, and, according to the map, this region was largely land during Jurassic times. Further (Neumayr, 1890, p. 419), Australia became separated from Asia and the rest of the world before the end of the Mesozoic time, that is to say, probably in the Cretaceous. This same idea is expressed by Koken (1893) in his map of the distribution of land in the latter period. Here we see that Asia and Australia were disconnected during the Lower as well as the Upper Cretaceous, but Australia comprises parts of New Guinea and the Sunda Islands as far as Java, Borneo and the Philippine Islands. In the older Tertiary, Koken includes Farther India into Asia, but then follows an archipelago and Australia remains isolated.

This wide connection, drawn by Neumayr between Asia and Australia during the Jurassic period, does not seem to be well supported, since marine Jurassic deposits have been discovered in the region of the Malaysian islands.<sup>1</sup> On the other hand, it is settled

<sup>1</sup> In Borneo, according to Krause and Vogel (*Samml. geol. Reichsmus. Leyden*, Vol. 5, 1897). The so-called "old slates" of Borneo are said to belong to

that a number of these islands possess very old, possibly Archaic rocks, which are overlaid directly by Tertiary beds, thus giving evidence of an intervening extended land period, during which no sedimentation took place. This has been demonstrated for the Philippine Islands, where an Eocene, Miocene and Pliocene series follows on top of old crystalline schists.<sup>1</sup> Similar conditions are said to prevail in Java (Martin). This, however, seems to be doubtful, since Verbeek and Fennema,<sup>2</sup> although they do not positively deny the possibility of the existence of Archaic rocks, pronounce the schists of Java Cretaceous, upon which, unconformably, Eocene and younger Tertiary beds are deposited. Archaic rocks are found in the Island of Amboina, where they are overlaid by Tertiary and Quarternary coral limestones. Between both there are, locally, older sediments of undetermined age.<sup>3</sup>

Aside from the supposed Cretaceous schists in Java, we know of beds of this period in Borneo, and, according to Kossmat (1895, p. 469 f.), only such that belong to the *Upper* Cretaceous, corresponding to the Ariyalur group (Senonian) of India. This fact is the more important, since, as Kossmat points out, it demonstrates that the Upper Cretaceous of southern India can be traced over Assam and Borneo to Japan and the Island of Sachalin (and thence to the western coast of North America). This indicates a continuity of the oceans in this direction, and consequently *Australia and Asia must have been disconnected in the Upper Cretaceous.*

From the foregoing, the conclusion may be drawn, that the geology of the Indo-Malaysian Archipelago is too scantily known to form an adequate idea of the former connection of Australia and Asia. This much, however, is settled, that large parts of this archipelago were once land, and the single islands were in many cases connected with one another. Verbeek (*l.c.*) has shown that of the Island of Java, in Miocene time (that is to say, very late), only the western part existed as a unit, and that it was continued eastward by a series of small islands. At the end of the Tertiary these

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the Lias (Martin, *ibid.*, Vol. 5, 1898; see also Molengraaff, G. A. F., *Geologische Verkenningstochten in Central Borneo*, 1900).

<sup>1</sup> Martin, *ibid.*, Vol. 5, 1896.

<sup>2</sup> *Geologische beschrijving von Java en Madera*, 1897. See also Verbeek, in *Petermanns geograph. Mitteil.*, 1898.

<sup>3</sup> Martin, K., *Reisen in den Molukken, in Amboin, den Uliassern, Seran und Buru. Geolog.*, Teil 1, Leyden, 1897.

islands became connected, and the whole was united with the continent of Asia; subsequently, a new (Quaternary) subsidence took place. According to Weber,<sup>1</sup> Celebes was connected in early times (beginning of the Tertiary?) with eastern Asia, but was separated later and dissolved into smaller islands, and assumed its present form at the end of the Tertiary. If changes of this character took place during the comparatively short Tertiary period, we are to expect, in Pretertiary times, much more varied conditions, and it is by no means impossible that the different islands, of which certain parts (for instance central Borneo) were never submerged after the beginning of the Mesozoic era, were variously and repeatedly connected with each other and the Asiatic mainland.<sup>2</sup> Such changing conditions existed probably during the whole of the Mesozoic time, and it seems, on account of the scarcity of Jurassic deposits, that during the Jurassic period land-conditions prevailed, although the land may not have had the extent assumed by Neumayr. It may have been similar during the Cretaceous period, but it seems that the land bridge began to dissolve; at least, in the Upper Cretaceous, we have positive indications that the connection between Asia and Australia was interrupted. This bridge probably was never again completely restored; the single parts of it, however, were not stationary in Tertiary times, and communicated with each other in various directions. These changing conditions are noticeable as far as New Guinea, and, as regards the latter island, we know through Haddon, Sollas and Cole,<sup>3</sup> that it is closely connected, tectonically, with Queensland. The archaic and palæozoic rocks of the "Australian Cordilleras" continue across the islands of Torres Straits into the southern part of New Guinea, which belongs undoubtedly to Queensland, and was separated from it at a very recent period. On the other side, the larger Sunda Islands (Sumatra, Java, Borneo) must have also been united with the Asiatic mainland in very recent time, as is positively shown by their fauna of higher land animals.

<sup>1</sup> Weber, M., *Zool. Ergebn. Reise Niederlaend. Ost-Indien*, Vol. 2, 1892; Vol. 3, 1894.

<sup>2</sup> According to Molengraaff (*Geologische Verkenningstochten in Central Borneo*, 1900), Borneo was submerged in Precretaceous times, but part of it was land in the Middle Cretaceous. At the end of the Cretaceous a subsidence took place, then again an elevation. The different parts of Borneo were subject in various degrees to these changes, which continued through the Tertiary.

<sup>3</sup> *Trans. R. Irish Acad.*, Vol. 30, 1894.

If the first sharp separation of Australia and Asia belongs to the *Upper Cretaceous*, it is consequent, for the *Parastacidae* and *Potamobiidae*, that their area of distribution, which before the beginning of the Upper Cretaceous extended over the Sino-Australian continent, was cut in two; of course, the ancestral forms occupying this old continent could not possibly have been divided into these two families, and their differentiation was directly connected with this separation of the geographic range. After that, there was a chance for either family to develop, since there was no longer communication between the Asiatic and the Australian stock. This forces us to the conclusion *that the ancestors of these two families must have existed before the beginning of the Upper Cretaceous time*, and that during the Upper Cretaceous the division into *Potamobiidae* and *Parastacidae* took place. It is impossible to place the origin of these families at a later period, since, as we shall see below, any crayfishes of late Mesozoic or early Tertiary age, in any part of the world, belong either to the one or the other family. Although there was at least a partial connection of Asia and Australia in Tertiary times, the two families never came into contact again: with the cause of this remarkable fact we shall become acquainted below.

With reference to the *Potamoninae*, their distribution over the Indo-Malaysian Archipelago is only partly explained by the assumption of a former continuous land bridge. The distribution of the freshwater crabs is by no means simple, and does not extend uniformly from eastern Asia to Australia, but there are numerous complications and peculiarities. In the first line, we have to emphasize the fact that only a single group, which is apparently highly specialized, the subgenus *Geothelphusa*, reaches the continent of Australia, and that this group (in its typical forms) is restricted to the Indo-Malaysian islands, and is wanting on the Asiatic continent. This is the more remarkable, since this group is most abundant just on the large islands of Sumatra, Java, Borneo, and extends northward over the Philippine and Loo Choo Islands to Japan. On the other hand, we have seen that the typical species of the genus *Potamon* (subgenus *Potamon*), which are found in both India and China, reappear in very closely allied forms in Java, Sumatra and the Philippines, but do not pass farther to the East. Then again, the subgenus *Potamonantes* possesses scattered stations



(probably strongly discontinuous) as far as New Guinea, and the same is the case in the genus *Parathelphusa*.

For the present, these very strange conditions defy explanation, and especially the eastern boundary of *Potamon* (sens. strict.) and the western boundary of *Geothelphusa* are puzzling. But this much we may say, that the distribution of the *Potamoninæ* over the Indo-Malaysian Archipelago is apparently due to the varying relations of the different islands between themselves and to the continents during the Tertiary period, and that it furnishes additional proof for the complexity of the changes that took place during this time in this region.

Another fact is to be especially mentioned. Among the *Potamoninæ* we do not have such a sharp separation of Australian and Asiatic types as we have found among the crayfishes: on the contrary, the species of *Geothelphusa*, found in northern and eastern Australia, are all closely related to those found in New Guinea and on the other islands. Also the different forms of *Potamon* (sens. strict.), found in Java and Sumatra, are very closely allied to continental species. All this points to the conclusion that the separation of the respective parts from each other, which brought about the present conditions, must be of comparatively recent date, and that at a time not very far remote from the present the distribution of land and water in this archipelago must have been considerably different from what it is now. Thus it seems that the causes of the distribution of the *Potamoninæ* in the Indo-Malaysian Archipelago are to be sought for in later times, presumably in the Tertiary, and that during this period, and possibly up to a very recent time, conditions prevailed here which—although they may not have amounted to a continuous land bridge—constituted a certain unstable connection between Asia and Australia. Probably there was a maze of larger and smaller islands, channels, straits and the like, which was not permanent in its parts, and changed repeatedly.<sup>1</sup>

Our final result on this question would be the following: South-eastern Asia was connected with Australia in the Jurassic, and probably also at the beginning of the Cretaceous period. In the

<sup>1</sup> According to von Ihering (1894, p. 406), Australia was connected with Asia during the Eocene and Oligocene. Hedley (1899) connects New Guinea with Australia in the later Tertiary; but a similar connection existed also in the Eocene, and through the latter Oriental elements were brought to New Guinea.

Upper Cretaceous, a sharp separation between both continents was formed, which continued possibly up to the Eocene. Then the connection was, at least partially, reestablished, but it was of a very changing character, which is expressed by the great complexity in animal distribution. These changing and unstable conditions prevailed all through the Tertiary, and up to the present time, and it is hard to trace them under the present imperfect state of our knowledge of the geology of the respective parts.

The Upper Cretaceous separation of Asia and Australia is expressed in the distribution of the *Potamobiidæ* and *Parastacidæ*: the formerly continuous area of their ancestors, which comprised in the Lower Cretaceous the Sino-Australian continent, was divided, about the middle of the Cretaceous, in a northern (East Asia-*Potamobiidæ*) and a southern (Australia-*Parastacidæ*) part. The varying conditions of the Tertiary are expressed in the distribution of the *Potamoninæ*; the details, however, cannot be made out, and further study of the freshwater crabs of these regions, as well as a more thorough study of the geology of these parts, is very desirable.

### 3. CONNECTION OF AFRICA AND INDIA.

The occurrence of crayfishes (genus *Astacoides*) in Madagascar has led us, as we have seen above (p. 295), to the assumption that there once existed a connection of this island with southern Asia (respectively with the Sino-Australian continent). The same connection is suggested by the distribution of the *Potamoninæ*, of which the subgenus *Potamonantes* is found in Africa as well as India. The Madagassian forms of the *Potamoninæ* (see above, p. 301) indicate a relation of this island to Africa, while a closer connection with India is not so striking. A genetic connection of the ranges of this subfamily in Africa and India by way of the Nile valley and Syria is improbable, although, geographically, this connection actually exists; this, however, is apparently due to secondary migrations, different branches of the subfamily, coming from India and Central Africa respectively, meeting in lower Egypt.

Thus we have to regard Madagascar as a stepping-stone between Africa and India, and, with reference to the *Potamoninæ*, its relation to Africa is closer than that to India.

This supposed connection is well known in zoogeography under the name of the *Lemurian* continent. Jacobi (1900, p. 169 ff.) quite recently has doubted this Lemuria-hypothesis, although he

introduces among his regions of dispersal, as a seventh, an Indo-African, which occupies this geographic position. He believes, however, that it is not correct to explain certain similarities of the faunas of India and Madagascar by a land-bridge, but prefers to accept the existence of a chain of islands, which permitted, in later Tertiary times, a migration of animals possessing the power of flight (Birds, Bats) in this direction. On the other hand, he grants a connection of Madagascar with Africa upward to the Miocene.

Jacobi's assumption of a series of islands instead of a continental connection from Madagascar to India seems to be well founded only for this particular time, the younger Tertiary. But the similarity of both faunas has apparently been underestimated by him, even if he takes into consideration only Mammals and Birds, and there are no doubt numerous relations between both parts among other animals not possessing the power of flight. This fact has been urged by Pilsbry (1894, p. xlv) for the *Helices*, and he says that Madagascar is much more closely allied to Ceylon and Australia than to South Africa.<sup>1</sup> The present cases offered by the genus *Astacoides* and within the family of the *Potamonidæ* are also very important for this question, since the idea of a migration of these forms over a chain of islands and across parts of the ocean is entirely out of question. Thus it seems that we have to assume a continental connection—if not during the later Tertiary—in earlier times.

The parts under discussion belong to the old Gondwana-land, which, according to Suess, existed in Palæozoic times, and was partially destroyed in the same period through the disconnection of Australia from it. Africa, however, remained intact, and formed an ancient table-land, to which was added as a peninsula the Lemurian bridge, which extended from Madagascar to India, and traces of which are preserved up to the Eocene (Suess, 1885, p. 538). This same peninsula is accepted by Neumayr for the Jurassic period, and is represented in his map; it is separated from the main part of Africa by a great gulf extending southward, the *Ethiopian Mediterranean Sea*, includes the present peninsula of India, and is not connected with the Sino-Australian continent, the Indian Gulf and the Strait of Bengal forming its northeastern shores. According to Neumayr (1890, p. 390), this Indo-Madagassian peninsula existed up to the end of the Cretaceous, and even

<sup>1</sup> In part, this may be due to old-Mesozoic, and even Palæozoic geography.

to the beginning of the Tertiary, but was destroyed in the older Tertiary (*l.c.*, p. 397).

The same view is expressed by Koken : for the Lower and Upper Cretaceous he gives to this peninsula about the same shape it had in the Jurassic (Neumayr), and in the older Tertiary he draws—instead of this continuous land-bridge—a chain of islands.

There are not many cases where we possess such ample evidence for the former existence of a land mass that has now disappeared, at least as regards such a remote epoch. The chief arguments for this land-bridge are taken from the character of the marine deposits found at the supposed southeast and northwest sides of this peninsula, and they are especially convincing for the Cretaceous period. The South-Indian Cretaceous, as it is found typically in the neighborhood of Pondichery, is known similarly developed in Madagascar and Natal, and belongs to the ocean to the east and south of this peninsula, while contemporaneous deposits of the western Indian Ocean (in East Africa) and in northwestern India are strongly contrasted to it, and are related to the Mediterranean type. We even may obtain further information as to the shape of this peninsula. According to Newton and Boule,<sup>1</sup> the Jurassic beds of the western coast of Madagascar belong to the Ethiopian Mediterranean Sea (possessing the Mediterranean type), while the Cretaceous beds (Cenomanian-Senonian) of the same parts exhibit the South-Indian type. This indicates that the Ethiopian Mediterranean Sea extended, during the Jurassic period, farther south than during the Cretaceous. The respective maps of Neumayr and Koken agree well with this : according to Neumayr, the southern extremity of Madagascar was united with Africa, while, according to Koken, the connection was situated at its northern end. This latter bridge continued to exist apparently during part of the Tertiary time. We have seen above that the connection of East Africa and India continued up to the very beginning of the Tertiary, and was destroyed soon after. This destruction, however, affected only the parts between Madagascar and India, while Madagascar itself remained connected with Africa : according to Jacobi, up to the beginning of the Miocene. Lydekker<sup>2</sup> is of the opinion

<sup>1</sup> See review by Boehm in *Neues Jahrb. f. Mineral., etc.*, 1897, Vol. I, p. 489.

<sup>2</sup> *A Geographical History of Mammals*, Cambridge, 1896.



that Madagascar became separated from Africa in the Oligocene or Miocene ; at the same time he connects Madagascar with India, and believes that this connection was not severed before the beginning of the Pliocene. In opposition to this we maintain that the connection of Madagascar with India was interrupted before that with Africa.

As the only remnants of this old bridge, the Seychelles have been preserved. They consist, according to Bauer,<sup>1</sup> chiefly of granitic rocks, which are accompanied by dikes and sheets of volcanic origin. Only traces of sedimentary rocks are found, and these point to a very old age. While we thus may safely take the Seychelles for a remnant of this old bridge—and this is confirmed by the presence of the East-African genus *Deckenia*—the other islands of the Indian Ocean (Chagos group, etc.), are coral-formation. They may rest upon the highest peaks of the submerged Lemuria, but the latter itself has disappeared here. Consequently the fauna of these islands—at least as regards freshwater Decapods—does not contain any forms indicating this old bridge, since they must have all been drowned.

The northeastern extremity of the Indo-Madagassian peninsula was formed by the present peninsula of India. According to Neumayr and Koken, this latter was separated, from the Jurassic to the older Tertiary, from the rest of Asia, that is to say from the Sino-Australian continent, by the Strait of Bengal, and, during the older Tertiary, India was, according to Koken (*l. c.*, p. 452), an *island* (also disconnected from Madagascar). It seems, however, that this separation of India from the rest of Asia was not so permanent as is believed by these authors. It is true, as regards its tectonic configuration, India has nothing in common with Asia, but it seems that there was a connection, at least at certain periods.

That the "Central Mediterranean Sea" of Neumayr extended during the Jurassic period across northern India to the Bengal Strait, separating India and Asia, seems to be correct, since no evidence to the contrary has been brought forth, and the latest investigations have shown that Jurassic deposits are widely distributed not only in the western but also in the central Himalayas.<sup>2</sup> But during a part of the Cretaceous, this strait does not seem to

<sup>1</sup> *Neues Jahrb. f. Mineral., etc.*, 1898, Vol. 2.

<sup>2</sup> See Griesbach, *Rec. Geol. Surv. India*, 26, 1893, and Diener, *Verh. k. k. geolog. Reichsanst.*, 1895.

have existed. Already Meddlicott and Blanford (1879, p. lx) have doubted that the plain of the Ganges river was covered by the Cretaceous ocean, and, although these authors generally disbelieve the existence of such a strait during Jurassic, Cretaceous and Tertiary times, Diener (*l. c.*, 1895) has demonstrated that there exists, in the central Himalaya mountains, an almost complete series of sediments from the Cambrian to the Eocene, among which Triassic and Jurassic beds are well represented, while Cretaceous beds apparently are missing and Eocene again is known. This is very much in favor of a connection of India with Asia during the Cretaceous. A very positive opinion on this question is expressed by Kossmat (1895, p. 463). He says that the Middle and Upper Cretaceous ocean of southern and eastern India was *not* connected over northern India with Europe.

Therefore, it seems to be well to assume only for the Jurassic period and for the Lower Cretaceous a separation of India and the Sinic continent; that is to say, during these times Lemuria (Madagascar-India) was a peninsula connected with Africa. In the Middle and Upper Cretaceous, this peninsula became united with the Sinic continent, forming a land-bridge between the latter and Africa. This connection, however, was apparently interrupted again in Eocene times. According to Neumayr (*l. c.*, p. 481), the Eocene deposits of the Central Mediterranean Sea (Nummulite-beds) are continued across the whole of northern India to the Gulf of Bengal (and farther to Java, Borneo and the Philippine Islands), and indicate thus a continuous ocean, which isolated India from the rest of Asia. Since, at about the same time (Eocene), the destruction of the Lemurian bridge took place, India became an island, as is first pointed out by Koken. In Post-Eocene times, this strait separating India and Asia disappeared, and we have, in northern India generally, at about this time (certainly from the Miocene upward), a regression of the ocean (see Meddlicott and Blanford, 1879, p. liii). The island of India was definitely joined to Asia and never again separated.

After the destruction of the connection of India with Madagascar, in the beginning of the Tertiary, of the southwestern parts of Lemuria only Madagascar remained, which was still connected, as a peninsula, with East Africa. Then this connection was also severed, but not before the Oligocene or the beginning of the Miocene. Thus the main outlines of the present distribution of land

and water were established at about the beginning of the Miocene. After the destruction of the Lemurian bridge in the Eocene, its northeastern portion, India, became part of Asia, while its southwestern portion, Madagascar, which at first remained a peninsula of Africa, became an island.

The application of these geographical results to the distribution of the freshwater Decapods is the following: First, we have to emphasize that before the middle of the Cretaceous it was impossible for the genus *Astacoides* to reach Madagascar. Since the separation of the Asiatic and Australian group of the crayfishes took place in about the Upper Cretaceous and since the morphological differentiation of the *Potamobiidæ* and *Parastacidæ* was connected with this separation, and further, since *Astacoides* must have immigrated into Madagascar from the Asiatic part of the old Sino-Australian continent, this latter process must have gone on shortly before the completion of this separation, that is to say, about the middle of the Cretaceous. This assumption is supported by the morphological characters of *Astacoides*, which are, in a certain degree, intermediate between the present two families and favor the view of an early separation from the original stock.

Thus there is nothing that prevents us to assume an immigration of *Astacoides* from southeastern Asia into Madagascar in the middle of the Cretaceous period. At a later time this does not seem to have happened, since, in this case, we should have different morphological characters in *Astacoides*. At an earlier time this immigration was impossible, since then India was not connected with the Sino-Australian continent. After the Eocene this migration was absolutely impossible, since then the land connection between India and Madagascar had disappeared.

Although we may thus fix the time of immigration of *Astacoides* rather exactly, there arise other questions. We want principally an explanation of the absence of similar forms in Africa itself, and for the absence of such in India and generally in southeastern Asia.

Regarding the *Potamoninæ*, their presence in Madagascar, and the close relation of the Madagassian forms to East-African, is easily explained by the former connection of Madagascar with Africa. The freshwater crabs of Madagascar thus indicate geographical conditions which are older than Miocene. The presence

of *Deckenia* on the Seychelle Islands connects also this group more closely with Africa than with India. Possibly this connection is identical with that over Madagascar, although *Deckenia* has not been found on the latter island.

The presence of *Potamoninae* in India, corresponding to the African type (subgenus *Potamonautes*), indicates the full development of the Lemurian peninsula, that is to say, conditions prevailing in the oldest Tertiary, if not earlier. *Potamoninae*, represented by forms which resembled the subgenus *Potamonautes*, must have existed at least in the beginning of the Eocene, and their distribution extended over Africa and the Lemurian peninsula, including India. During the Eocene this range was separated into two parts, an African (to which Madagascar belonged) and an Indian, and, beginning in the Miocene, the *Potamoninae* had a chance to expand over southern and eastern Asia (Farther India and China<sup>1</sup>). At the same time they availed themselves of the various and changing connections within the region of the Indo-Malaysian archipelago, occupying the latter and reaching Australia. The opening of this region of dispersal offered to this group a new opportunity for a rich development, and the origin of the subgenera *Potamon* and *Geothelphusa* was probably the outcome of it.

We cannot leave this chapter without saying a few words on the Arabian region of dispersal of Jacobi. This extends from north-eastern Africa across Arabia to India. Jacobi mentions the similarity of the Siwalik-fauna of India with the Ethiopian. This, consequently, refers to a very recent period, the later Tertiary. Before this time, in the older Tertiary and in the Mesozoic, this connection is out of question. The *Potamoninae*, which, as we have seen, existed in the older Tertiary, show no trace of this connection across Arabia, and, as we shall see below, our knowledge of the ancient geography of these parts is a very fair one. Arabia itself formed originally a part of Africa, and the Red Sea did not exist at all in the earlier Tertiary, it being quite recent (see below). Toward the north, northeast and east Arabia was circum-

<sup>1</sup>There was, possibly, an earlier chance to reach the Sinic continent, in Upper Cretaceous times, and I am inclined to believe that the discontinuous localities of *Potamonautes* (and *Parathelphusa*) in the Indo-Malaysian archipelago point to an immigration of these forms that precedes in time that of *Potamon sens. strict.*



scribed by sea—the Central Mediterranean Sea and the Ethiopian Gulf of Neumayr. A connection with India in this direction, and a migration of *Potamoninae* from India to Africa (or *vice versa*) by this route was then impossible.

Further, I should like to point out that we have to be careful about this Indo Madagassian bridge. A case which has occurred to me, and which might lead to misinterpretation, is furnished by the distribution of the Reptile-family *Chamaleontidae*. According to Gadow,<sup>1</sup> this family is found in Africa, Madagascar and India, a distribution which is quite analogous to that of the *Potamoninae*, and might induce us, at the first glance, to trace it back to this old Indo-Madagassian connection. A closer study, however, reveals the fact that the *Chameleon* of India has nothing to do with the Madagassian species, but is related to the form widely distributed in North Africa, Syria and Asia Minor. Here the connection apparently goes from North Africa over Syria and Arabia to India, and this distribution belongs to a much later period when Lemuria no longer existed.

#### 4. CONNECTION OF NEW ZEALAND WITH AUSTRALIA.

We have seen that a genus of the family *Parastacidae*, *Paranephrops*, is found in New Zealand, and this fact points to a former connection of these islands with Australia. We further are to pay attention to some additional facts, which, although they do not seem to be sufficiently established to be accepted without comment, are apt to throw some light upon this connection.

First, according to Huxley (*Tr. Zool. Soc.*, 1878, p. 771), *Paranephrops* is said to be found in the Fiji Islands.\* This locality is supported by two specimens in the British Museum, which are in a very bad condition; moreover, there is no report as to the authenticity of the locality, and the genus has never again been reported from these islands.

Further, Nobili (1899) describes from southern New Guinea a genus and species, *Astaconeophrops albertisi*, which is said to be closely allied to *Paranephrops*. It is impossible, however, to control the systematic position of this form, since only external characters are given, and the most important one, the branchial

<sup>1</sup> Gadow, H., "Amphibia and Reptilia," in *The Cambridge Natural History*, Vol. 8, 1901, map, p. 568.

formula and shape of gills, is entirely unknown; a figure of this very important form is also missing.

But taking it for granted that the genus *Parastacus* itself is found in the Fiji Islands, and that *Astaconephrops* in New Guinea is closely allied to it, this would indicate a connection of New Zealand with Australia by way of Fiji Islands and New Guinea. This assumption appears, judging alone from this material, very poorly supported, but it agrees well with other known facts which have led to a similar theory. †

According to Hedley (1899), New Zealand was connected with Australia in the following manner (see map, *l. c.*, p. 404). From North Australia and New Guinea, which were united, a peninsula extended over the Solomon Group and the New Hebrides, where a smaller peninsula branched off in the direction toward the Fiji Islands; and, farther, this main peninsula extended over New Caledonia, Lord Howe Island to New Zealand. Hedley calls this the "Melanesian Plateau," and we may name it conveniently the Melanesian Peninsula or *Melanesia*. As to the time of existence of the latter Hedley does not express himself very positively, but according to von Ihering (1894, p. 406), New Zealand and the Fiji Islands became separated from Australia before the Eocene, or, as may be gleaned from other places in his text, at the beginning of the Eocene.

The views of these two authors are founded exclusively upon zoogeographical evidence, and we see that the genus *Paranephrops* of New Zealand is apt to furnish additional support to Hedley's Melanesian Peninsula. That this peninsula was disconnected from Australia, not later than in the Eocene, also agrees with our material. We have seen above that forms of the *Parastacoid* type must have existed in Australia as early as in the Upper Cretaceous, and thus nothing opposes the assumption that they immigrated into New Zealand in Pre-Eocene times.

Examining the tectonic and geological side of the question, we have to refer first to the views propounded by Suess (1888, p. 181 ff.). According to him, the Alps of New Zealand are a comparatively old range, which existed probably as early as in Jurassic times, and, further, he points out (*l. c.*, p. 203 ff.) the analogy in the structure of New Caledonia and New Zealand. For the rest, the islands between New Caledonia and New Guinea are too poorly known in this respect, and, therefore, we cannot say anything

about a possible tectonic connection of these parts. Neumayr, however (1890), draws in his map of the Jurassic continents, mentioned repeatedly above, a peninsula, which is connected with his Sino-Australian continent, and which corresponds closely to Hedley's idea of Melanesia. This peninsula is missing in Koken's map (1893) of the Cretaceous continents, and even New Zealand is not given as land there. But Koken does not seem to have paid much attention to these parts of the earth's surface in Cretaceous times, since it seems quite sure that at least parts of New Zealand were land then. In the Older Tertiary, New Zealand and New Caledonia were islands, according to Koken, while Australia extended far to the east, including Lord Howe Island.

Although, in general, the geological evidence for the connection of New Zealand with Australia is very scarce, we certainly have to assume it according to the characters of the fauna and flora of New Zealand, and the material at hand points distinctly to the fact that this connection was interrupted at a comparatively early period. Thus there is nothing that is opposed to the view of von Ihering, that the final isolation of New Zealand took place not later than the beginning of the Eocene, and there is no objection to the demonstration on the part of Hedley that this connection with Australia was by way of New Caledonia and New Guinea. Our present case, the distribution of *Paranephrops* in New Zealand, fits well into this theory: this genus reached New Zealand in Pre-Tertiary times, probably in the Upper Cretaceous, and very likely by the way indicated by Hedley; since the Eocene it has become isolated on this island group.

##### 5. CONNECTION OF SOUTH AMERICA WITH AUSTRALIA (RESP. NEW ZEALAND).

The genus *Parastacus* in the temperate and subtropical parts of South America points to a connection of this continent with those parts in which allied forms are found, namely, with Australia and New Zealand. Numerous instances of a similar distribution, which suggest a relation of the same parts, are known, not only among land and freshwater animals, but also among the marine littoral fauna. This remarkable fact has been noticed at a very early time, and has suggested various theories, which have been reviewed and classified by the present writer (Ortmann, 1901). The views of the majority of the later authors now agree more or

less in that this connection is placed across the Antarctic continent, and this idea is chiefly supported by Hedley (1895, 1899), von Ihering (1891, 1894), Osborn (1900), Pilsbry (1894), and Ortmann (1901, 1902).

While Pilsbry only generally expresses the opinion that the supposition of an old Antarctic continent connecting the respective parts of the present southern continents would furnish the conditions necessary for the explanation of the zoogeography of the land-mollusks, and while Osborn only tries to give an approximate idea of the mutual relations of these land-masses by pointing out that a subsidence of the ocean level of a certain amount would connect these parts, von Ihering (1894, p. 438) gives a more detailed theory of this connection. He unites not only South America over Antarctica with Australia, but continues this (Mesozoic) land mass beyond the Indo-Malaysian islands to east Asia, thus including the Sino Australian continent discussed above. He calls this vast continent by the name of *Archinotis*.

As to the details of the special connection of Australia and South America, Hedley's opinion is the most important; according to him (1895, p. 6), during Mesozoic and older Tertiary times a stretch of land extended from Tasmania over the South Pole to Terra del Fuego; the shore line of this land (Antarctica) formed a wide gulf between Tasmania and Cape Horn, and approached the Pole. This land-bridge, however, was not very solid, but was subject to various changes resulting in a repeated breaking up and becoming reunited of the different parts. As regards New Zealand, he believes that during the *Tertiary* time it was not directly connected with Antarctica. In another paper, however (1899, p. 399), Hedley also assumes a connection of New Zealand with Antarctica, but this was of an older date than that from Australia over Tasmania to Antarctica, and consequently is to be placed in the Mesozoic time.

That Australia was once connected with Antarctica, especially with what is now called Wilkes' and Victoria Land, can be imagined as possible on tectonic grounds. Australia itself consists, according to Suess (1888, p. 188 ff.), in its eastern part of a very old range of mountains, running in a north-southerly direction; its larger western part is an old Archaic and Palæozoic plateau (part of Gondwana Land). Both parts are fractured and cut off toward the south, and the southern parts have disappeared; a line



of faults at the southern margin of the Australian Plateau indicates that Australia undoubtedly extended once farther southward, in the direction toward Antarctica. Whether it was really united with the latter cannot be said positively, chiefly because the geological structure of Wilkes' Land is entirely unknown.

The time of the subsidence of the southern parts of the old Australian continent can be determined according to the conditions known to exist on the shores of the great Australian Bight. Here, on the foot of the broken edge of the Australian Plateau, a series of Tertiary deposits is found, the age of which is not yet positively ascertained, but which seem to belong to both the older and younger Tertiary. The fact that no older (Mesozoic) beds are found in this region seems to indicate that such were not deposited, and that means to say that up to the end of the Mesozoic time the southern part of the Australian Plateau had not subsided, and that this process took place at the very beginning of the Tertiary.

Thus we have reason to believe that the connection of this part of Australia (the western plateau) with Antarctica *existed up to the end of the Mesozoic time.*

The Tertiary deposits of the south coast of Australia are lacking from Tasmania along the eastern coast of Australia; here is a fracture toward the south and east, the age of which cannot be determined at present. Hedley believes that there was here a connection with Antarctica that persisted up into the Tertiary (over Tasmania), but he gives no geological evidence for it. It is entirely unknown whether the East Australian Cordilleras find a continuation in Antarctica. So Hedley's assumption may or may not be correct.

Another tectonic line in these regions has been pointed out by Gregory.<sup>1</sup> He also emphasizes the former southward extension of the Australian Plateau; but besides, there seems to be, according to him, a very important tectonic line marked by the volcanoes of New Zealand and Victoria Land, and this, possibly, finds its continuation in the volcanoes of the region of Graham Land, and passes thence over Terra del Fuego to the South American Cordilleras. Of course, this is no evidence at all that this line from New Zealand over Antarctica to South America has ever been a continuous mountain range actually connecting these parts, but the

<sup>1</sup> *Nature*, Vol. lxiii, 1901, pp. 610-611, with map, p. 611.

existence of such a line would in a large degree facilitate the imagination of such a connection, and would force us—if we have other evidence pointing to a former connection of these parts—to construct this old land-bridge nowhere else but along the direction of this line. That is to say, the connection of Australia and New Zealand with South America, which is probable on account of certain facts in the distribution of life, *was across the Pole, and not in lower latitudes in the southern part of the Pacific Ocean*, as accepted by some authors.

The tectonic connection of Graham Land with Terra del Fuego, indicated by Gregory, is much emphasized by Fricker.<sup>1</sup> According to him, it is formed by the arc of islands running from Terra del Fuego over South Georgia and the South Sandwich Islands to Graham Land. This line, however, again indicates only the general direction of this possible connection, but does not give any hints as to its actual existence, nor to the possible time of it.

We know that a large part of South America (the Brazilian Plateau, see below) is a very old continental mass, which extended southward into northern Argentina, but not into Patagonia. What is now the chain of the Cordilleras was certainly ocean during Mesozoic times, since here we find Jurassic and Cretaceous deposits largely developed, and the latter have been traced far to the south and over almost all of Patagonia; the Tertiary beds of southern Patagonia rest, wherever this has been observed, upon Cretaceous deposits.<sup>2</sup> The Patagonian Cretaceous, in its upper divisions, consists of rocks formed apparently under continental conditions (littoral, freshwater, or eolian), and these latter (Guaranitic beds) were subject, after their deposition, to erosion, indicating a land period at the close and after the Cretaceous. Thus, there seems to have been an upheaval, beginning at the end of Mesozoic time and continuing into the Tertiary; during the Eocene these regions probably were land to a large extent.<sup>3</sup>

West of the Mesozoic beds known in the tract of the Cordilleras there are, in the so-called Coast Cordilleras of Chili, rocks of another character; they are apparently metamorphic, but their age is disputed. According to Steinmann,<sup>4</sup> they are Mesozoic; and

<sup>1</sup> *The Antarctic Regions*, London, 1900, p. 140 ff.

<sup>2</sup> See Hatcher, J. B., in *Amer. Jour. Sci.*, Vol. ix, 1900, p. 95 ff., and Ortmann, *Rep. Princeton Exped. Patagonia*, Vol. iv, Part 2, 1902, p. 285.

<sup>3</sup> See Ortmann, *l. c.*, p. 317.

<sup>4</sup> *Neues Jahrb. f. Mineral.*, etc., Beil., Bd. 10, 1895, p. 6.

according to Wollf,<sup>1</sup> they are at least older than Jurassic. This coast range is continued southward across the Straits of Magellan, and forms the southwest and south coast of Terra del Fuego, where similar rocks are found, and here it curves more and more in a west-easterly direction.

However, the old and even Mesozoic age of the rocks composing this chain is not generally accepted, and also the identity of the Fuegian rocks with those of Chili has been doubted; Norden-skjöld,<sup>2</sup> for instance, takes the metamorphic rocks of the outer (western and southern) side of Terra del Fuego for Cretaceous.

Thus we see that there is considerable uncertainty about the configuration and geology of southern South America in the Mesozoic era; but this much seems to be settled, that the Chilean coast range existed as early as the Cretaceous period,<sup>3</sup> and that the Cordilleras in Terra del Fuego were not formed later than in the Cretaceous. It is just this latter chain that continues over Staten Island, South Georgia, etc., and finally connects with Graham Land; and if there was connection at any time, it was by this way and in the Cretaceous.

Further, there is no doubt that at the end of the Cretaceous period large tracts of Patagonia became dry land, and the maximum of land extension falls probably in Eocene times.

Consequently we have to put the chief connection of the southern parts of South America with Antarctica at the end of the Cretaceous and in the Eocene. But we are to emphasize here that thus far we have been able only to connect the Chilean coast range with Antarctica. According to von Ihering, this connection also comprised old Archiplata (the Brazilian mass) and existed during

<sup>1</sup> Wollf, F. von, in *Zeitschr. deutsch. Geolog. Gesellsch.*, Vol. 51, 1899.

<sup>2</sup> Geological Map of the Magellan Territories (Svenska Exped. till Magellans-land, Vol. 1, No. 3, 1899).

<sup>3</sup> And possibly earlier. Burckhardt, C. ("Traces géologiques d'un ancien continent Pacifique," in *Rev. Mus. de la Plata*, Vol. 10, 1900, p. 177 ff.), has brought forth some evidence for the assumption that in Chili, west of the present Cordilleras, which were sea during the Upper Jurassic, there existed a continent, the eastern shore of which was formed by the Chilean coast range. There is no means, however, of deciding how far this Jurassic continent extended to the west. The Jurassic age of this range, together with the corresponding rocks of Terra del Fuego, etc., is quite likely if Gregory's theory of the tectonic connection with New Zealand is correct; also, the mountains of New Zealand are said to possess Jurassic age (see above, p. 334).

the whole Mesozoic era, but this seems to be doubtful; at any rate, a connection of the southern and western land in South America (Chilean coast range) with the rest of South America is improbable during a large part of the Cretaceous time, since marine deposits belonging to this period are found in the present Cordilleras, indicating separation by sea. This sea apparently was a strait running in a north-southerly direction, and coinciding approximately with the present direction and location of the Cordilleras. This strait became dry at the beginning of the Tertiary, in the Eocene, since Tertiary deposits are not found here, and thus a connection of the main mass of South America, the Brazilian Plateau, was formed in an east-westerly direction with the Chilean coast range. This completed the connection of South America with Antarctica in Eocene times, and, in our opinion, is very important and serves to explain the numerous zoogeographical peculiarities of South America.

To sum it up, we are justified to draw the following conclusions: There is nothing that opposes, on tectonic or geological grounds, the assumption of a connection of *Australia with Antarctica*, as far as the evidence at hand goes. *This connection belongs pre eminently to the Mesozoic time*, and was interrupted, at least for a large part, at the end of this era, definitively at the beginning of the Tertiary. We have no positive evidence for a *permanent Mesozoic connection of South America and Antarctica* (but such may have existed); *but a connection of these parts is very probable at the end of the Mesozoic time, and especially during the Eocene between the Antarctic lands and the old Brazilian mass*; the southernmost parts of South America (southern Patagonia and Chili) were connected in the Cretaceous with Antarctica, forming part of it, but were still separated from Archiplata. In the Eocene they were also connected with the latter. This latter union was brought about by the upheaval of the Cordilleras, which began toward the close of the Cretaceous and continued almost all through the Tertiary.

We are not going to follow up this idea any further, although we believe that it will prove to be very important with regard to the origin of the South American fauna. For our present purpose, the explanation of the presence of the genus *Parastacus* in South America, we arrive at the conclusion that the family *Parastacidae*, which existed, as we have seen, during the Upper Cretaceous period in Australia, had a chance, during this same time, to spread



into Antarctica, and consequently into the southernmost parts of America (Chili). Thence it extended, in the beginning of the Tertiary, into Northern Argentina and Southern Brazil (Archiplatea). This west-easterly direction of migration from Chili to Brazil is in a certain degree expressed in the present distribution of the genus *Parastacus*, and the distribution of the genus *Æglea* seems to have been formed under similar conditions, although its Antarctic origin does not seem probable. The present southern boundary of *Parastacus* is possibly due to the present climatic conditions, it having died out in the south of Chili and Patagonia on account of the unfavorable climate of these parts.

The fact that the genus does not extend northward into the truly tropical parts of Brazil needs further explanation. We shall return to this later.

The presence of the genus *Parastacus* on both slopes of the Cordilleras (even the identical species is found in one case on both sides, and in this respect the genus *Æglea* agrees with *Parastacus*) points to a time when the Cordilleras had not yet attained their present elevation. As v. Ihering has shown, for many groups of animals this chain forms a very sharp barrier, and it does not seem probable that these freshwater Crustaceans are able to cross these high snow and ice-covered mountains. In the case of *Parastacus agassizi* a shifting of the continental divide (by the capturing of the headwaters of a stream belonging to the drainage of the opposite side) cannot explain its presence on both slopes, since in this region the original divide seems to be intact (the waters of Lake Nahuel Huapi drain to the Atlantic Ocean). Thus also this fact is in favor of an early origin of the distribution, since the elevation of the Cordilleras, although beginning at the end of the Cretaceous, did not attain its maximum till about the Miocene.<sup>1</sup>

#### 6. CONNECTION OF THE WEST INDIES WITH CENTRAL AND SOUTH AMERICA.

We have seen above that *Cambarus cubensis* of Cuba finds its most closely allied species in *C. mexicanus* of Mexico. Similar conditions prevail among the species of *Pseudothelphusa* from the Greater Antilles, two species (*P. americana* and *terrestris*) being also found in Mexico. On the other hand, the six species of the

<sup>1</sup> According to Hatcher, the Miocene Patagonian and Santa Cruzian beds are largely disturbed in the region of the Cordilleras in Southern Patagonia.

genus *Epilobocera* (from Cuba to Porto Rico and Sta. Cruz) are restricted to these islands and do not possess any closely allied forms on the mainland, although there is no doubt that they are distantly related to the Central and South American freshwater crabs and must have been derived from these parts. Thus it seems that we are to distinguish two groups among the freshwater Crustaceans of the Greater Antilles, pointing to two migrations from the mainland of Central America—an older one, represented by *Epilobocera*, the higher age of which is supported by the fact that this genus possesses in some respects the most primitive characters among the whole subfamily, and a younger migration, represented by the identical species of *Pseudothelphusa*. It is doubtful to which of these groups *Cambarus cubensis* belongs, since it is different from but closely allied to a Mexican species.

Entirely different in its relations is the *Pseudothelphusa* (*P. dentata*) of the Lesser Antilles. This one points beyond doubt to South America (Trinidad and Venezuela) and bears no relation at all to the Greater Antilles, not to speak of Mexico.

The geology and tectonics of the West Indies and Central America are only poorly known, but lately some very important contributions have been published. Nevertheless, the conditions prevailing here are far from being clear, and the opinions of different authors vary frequently. This much seems to be sure, that the history of this section of the earth is a very varied and complex one.

In the first line we are to consider the fact that the general features of the main mountain ranges of Central America and the West Indies possess much in common and differ sharply from both North and South America. Especially the west-easterly strike of the old ranges of Central America (Guatemala, Honduras), as well as of the Greater Antilles (Cuba, Hayti, Porto Rico, Jamaica), is very remarkable (see Suess, 1885, p. 698 ff.), and indicates a former tectonic unit. According to Hill (1898), old rocks exhibiting the same west-easterly strike are found largely distributed also in Nicaragua and Costa Rica, and, further, in the region of the Isthmus of Panama, especially to the east of Colon, in the Cordilleras of San Blas. Furthermore, the whole northern shore of Venezuela, from Puerto Cabello to the northeastern end of the island of Trinidad, consists of old granitic ranges with the same strike. All these observations, although apparently incomplete and scattered, most likely

indicate that this whole region, *i.e.*, Central America, the Greater Antilles and the northern coast of South America, possesses an "old basement of granitic rocks of earlier age than the oldest determinable sedimentary rocks" (Hill, 1898, p. 241), which, in its west-easterly strike, differs entirely from the present mountain ranges of North and South America, and it is possible that these parts once formed a unit, a solid continental mass. As to the age of this continent we may form an idea if we consider that (Hill, *l. c.*, p. 243) Jurassic beds are absent in this region, so that during this time at least this continent was in existence. The same seems to be true for a large part of the Cretaceous time. Cretaceous deposits are wanting in Central America from Costa Rica eastward in the Isthmian region and on the West Indian islands.<sup>1</sup> On the other hand, Cretaceous beds are found in Guatemala to the north of the old granitic mountains. They are also extensively developed to the south and southeast of the old granites in Colombia and Venezuela (see below), and thus it seems that this old continent was washed to the north as well as to the south by Cretaceous seas.

But at about this time (toward the end of the Cretaceous) this old Mesozoic Antillean continent must have been destroyed, probably by the formation of the Caribbean Sea. We do not know much about the exact time when this happened, but we know that the subsidence forming this basin within this old mass was accompanied by a faulting along the margins of the subsiding area. This fault is clearly seen at the coast of Venezuela, where, according to Suess (1885, p. 687 f.), the old coast range breaks off to the north. The fact that within the whole region of the Caribbean Sea no Cretaceous deposits are positively known makes it very probable that the formation of this depression falls at the end of the Mesozoic age.<sup>2</sup>

<sup>1</sup> There are, however, Pre-Tertiary sediments, belonging possibly to the uppermost Cretaceous, in some of the Greater Antilles (see Hill, *Amer. Journ. Sci.*, Vol. 48, 1894, p. 197); but this again demonstrates that sedimentation in these parts did not begin till the very end of the Mesozoic time.

<sup>2</sup> There are Cretaceous deposits of Lower Senonian age in western Venezuela which possess the Mediterranean type (see Gerhardt, in *N. Jahrb. Mineral.*, etc., Beil., Bd. 11, 1897, p. 87). This possibly is the first indication of the existence of the Caribbean Sea. But we must not forget that the Lower Cretaceous of Colombia and Peru also exhibits Mediterranean character, which is due, no doubt, to the Orinoco connection. It is remarkable that the relation of these Lower Cretaceous beds to Texas is not very evident, they probably being sepa-

In subsequent times, at the beginning of the Tertiary, the Caribbean Sea must have existed, since Tertiary deposits are largely developed in this region, not only on the Antilles but also on the Isthmus of Panama. It seems that in the beginning of the Tertiary the old Antillean continent was divided into two main sections—the Greater Antilles with Honduras and Guatemala to the north, and the coast range of Venezuela to the south. The remnants of this continent in the Greater Antilles and Central America remained first in a large part land, but apparently they were subject to various changes during the Tertiary period and subsided and were elevated repeatedly.

We have seen that the geographical distribution of certain freshwater Decapods demands in the first line a connection of the Greater Antilles with Mexico, and according to the foregoing considerations this connection can have been situated only in the direction over Honduras and Guatemala. We have further seen that a Mesozoic connection of these parts is very likely, and that the connection of Venezuela with Central America existed almost up to the end of the Cretaceous. As we shall see below, we have reason to believe that the freshwater crabs reached Venezuela in the second half of the Cretaceous, and consequently it was also possible for them to extend during this time into Central America (and Mexico). If the latter parts were then or later connected with the Greater Antilles, this would account for the presence of the most primitive genus of the subfamily, *Epilobocera*, in these islands. On the other hand, *Potamobiidae* were probably present at the end of the Cretaceous times in western North America. These parts were connected with Central America in this period, Mexico being dry land, and thus there was also a chance for the *Potamobiidae* (represented here by *Cambarus*) to reach finally the Greater Antilles. Therefore we reach the conclusion that the first immigration of freshwater Decapods into the Greater Antilles, represented by *Epilobocera*, belongs to the end of the Cretaceous or the beginning of the Tertiary, and that *Cambarus cubensis* possibly also belongs to it; but since this form is a true *Cambarus*, although a primitive one, I should prefer to put its immigration rather in the Tertiary than in the Cretaceous.

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rated from Texas by the Antillean continent, while the Upper Cretaceous of Western Venezuela shows close affinity to Texas, the Antillean continent having disappeared.



The same zoogeographical question has been investigated by Simpson<sup>1</sup> with reference to the land and freshwater Mollusks. He points out that among this group in the Greater Antilles we find quite a number of species which are identical with species from Central America and Mexico (list p. 488, *l. c.*), and, besides, there are in both parts numerous and more or less closely allied forms. Simpson does not distinguish very sharply these two categories, identical and allied forms, but they correspond very likely to the same two groups among our Decapods.

Now Simpson draws the following conclusions: Sometime during the Eocene the Greater Antilles were elevated and connected with each other and with Central America by way of Jamaica (and possibly across the Yucatan channel). Then a period of subsidence followed, culminating in the Miocene and submerging the Antilles with the exception of their highest parts, which ended the connection with Central America. In Postmiocene times the Greater Antilles were elevated again and attained their present shape.

For the Lesser Antilles the matter was entirely different. These islands did not exist at all in Eocene times or were submerged subsequently, since their Mollusk-fauna, with the exception of a few forms which may have reached them by drift, shows no affinities to that of the Greater Antilles. After the formation of this island chain, during the course of the Tertiary,<sup>2</sup> it was populated chiefly from South America, and, as Simpson believes, by drift. The South American (Venezuelan) origin of the fauna of the Lesser Antilles is also confirmed by our material. *Potamocarcinus dentatus* points directly to Trinidad and Venezuela and not to the Greater Antilles. I should doubt, however, that this species has reached these islands by drift, and I am inclined to assume a continental connection of these parts, which may have been of short duration, during the later Tertiary. I am loath to believe that it is possible for these freshwater crabs to be transported across salt water, and the fact that one species is found on the islands of Guadeloupe, Dominica, Martinique, St. Lucia, another in Trini-

<sup>1</sup> Simpson, C. T.: "Distribution of the Land and Freshwater Mollusks of the West Indian Region, and their Evidence with regard to Past Changes of Land and Sea" (*Pr. U. S. Nat. Mus.*, Vol. 17, 1895).

<sup>2</sup> That these islands were formed during the Tertiary is also the opinion of Hill. See Report by Robert T. Hill on the volcanic disturbances in the West Indies in *The Nation, Geograph. Magaz.*, Vol. 13, 1902, pp. 229, 240, 265.

dad and a third in Venezuela is entirely opposed to the drift theory, since under the latter we ought to expect only *one* species in this whole region.

Simpson's theory of the origin of the West Indian faunas is supported exclusively by zoogeographical evidence, and, as we have seen, it agrees admirably with the facts presented by the Decapod Crustaceans. But the various changes undergone by the West Indian islands have been investigated also from a geological and physiographical standpoint. I shall disregard the views of Spencer<sup>1</sup> on the Antillean continent, which are certainly exaggerated, since he makes this whole region land during the Pliocene, even including the floor of the Mexican Gulf and the Caribbean Sea. According to him, the Pliocene land would have been elevated above the present level to the amount of one and one-half to two and one-half miles, and this would result in a wide connection of both North and South America with the Antillean land. But this is simply impossible. If such a land connection had existed in Pliocene times, it should have left not only unmistakable traces in the present fauna of the Antilles, but the Antillean fauna ought to be practically identical with that of the southern parts of North America and the northern parts of South America; but this is by no means the case. Nevertheless, one of the items in Spencer's theories is important for our purposes. This is the assumption of a Pliocene elevation of these parts, succeeded by the opposite movement at the end of the Pliocene and in the Pleistocene.

On the other hand, Hill<sup>2</sup> assumes for Cuba a subsidence at the beginning of the Tertiary. This is followed, in the older Pleistocene, by a rapid elevation, continuing more or less continuously up to the present time. This late Tertiary and recent elevation influenced also the neighboring parts of the Gulf of Mexico and the Caribbean Sea, and Hill concedes that it was possible that Cuba extended then as far as Yucatan, thus connecting with Central America.

The views of Hill and Simpson agree only in part as to the general movements of these regions. Simpson assumes an Eocene elevation and land connection, while Hill's elevation is Pleistocene. But it is quite possible that both are correct. We have

<sup>1</sup> Spencer, J. W.: "Reconstruction of the Antillean Continent" (*Bull. Geol. Soc. America*, Vol. 6, 1895).

<sup>2</sup> *Bull. Mus. Harvard*, Vol. 16, 1895.

seen that our material points to a double connection of Cuba and Central America, an older and a younger one, and it is very likely that the one is identical with Simpson's and the other with Hill's. Between them there is a period of subsidence, the maximum of which belongs probably to the Miocene. This agrees with both Hill's<sup>1</sup> and Simpson's views. The upheaval assumed by Hill for the end of the Tertiary and the corresponding connection with the mainland has been indicated previously by Neumayr (1890, p. 541), and the same theory is proposed by Spencer. And, further, Simpson also advocates a Postmiocene elevation, which, however, did not result in a connection with Central America.<sup>2</sup>

According to the foregoing, the history of the development of the Central American and West Indian region, as supported by the freshwater Decapods, is the following :

*Central America, the West Indies and the northern margin of South America formed in the Mesozoic period (certainly during Jurassic and Cretaceous) a continental mass (Antillean continent), which was bounded by sea to the north and south. This continent broke up at the end of the Cretaceous, the chief factor in its destruction being the formation of the Caribbean Sea. The northern remnant of this continent, consisting of the Greater Antilles and parts of present Central America, probably remained a unit up to the Eocene. But at the end of the Eocene and during Oligocene and Miocene the connection between the Greater Antilles and the mainland was severed. But it was re-established toward the end of the Tertiary (Pleistocene) and again destroyed in the recent time.*<sup>3</sup>

<sup>1</sup> The subsidence of Cuba at the beginning of the Tertiary, mentioned by Hill (*l. c.*, 1895), refers to the beginning of the *Cuban* Tertiary—that is to say, to deposits including Eocene and Miocene. See Hill, in *Amer. Journ. Sci.*, Vol. 48, 1894, p. 201.

<sup>2</sup> T. Wayland Vaughan (*Science*, January 24, 1902, p. 148) doubts the Pleistocene connection of Cuba with the mainland, since the recorded finds of Pleistocene Mammals in Cuba are open to discussion, and possibly did not come from this island. But the cases of identical species among the Mollusks, mentioned by Simpson, and the identical species of freshwater crabs discussed here are beyond doubt, and the tendency of the evidence furnished by them is in the same direction as that of the Mammals. We do not believe, however, in a connection of Cuba with North America, but with Central America. (Simpson accepts an Eocene connection with the *island* of Florida, by way of the Bahamas, which ended in the Miocene.)

<sup>3</sup> This only partly agrees with what we know about the history of Jamaica.

It seems that part of the freshwater Decapods (the identical species) found their way from Central America to the Greater Antilles during the Pleistocene connection, while the genus *Epilobocera* reached the same parts in much older times, in the beginning of the Eocene or even at the end of the Cretaceous. How all these forms were able to get into Central America we shall discuss below.

To which of the two immigrations *Cambarus cubensis* belongs remains doubtful. I am inclined to classify it with the older (Eocene) immigration.

The freshwater crab of the Windward Islands, *Potamocarcinus dentatus*, confirms the view of Simpson that these islands and their fauna have little to do with the Greater Antilles, but rather that they are related to South America. But, while Simpson believes that the (late Tertiary) population of the Lesser Antilles was accomplished by drift, I believe that a land connection is indicated.

#### 7. CONNECTION OF SOUTH AMERICA AND AFRICA.

The presence of freshwater crabs belonging to the family of the *Potamonidae* in the Old World (subfamilies *Potamoninae* and *Deckeniinae*), as well as in the tropical parts of the New World (subfamily *Potamocarcininae*), has led us above (p. 310) to the assumption that there was once a land connection between South America and the West Indies on the one side and Africa on the other. Similar zoogeographical facts have been emphasized chiefly by von Ihering (1891, p. 438, and 1894, p. 406), and, according to him, "all affinities of the freshwater fauna of northern South America direct us to Africa." He believes (we shall discuss this later) that the

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Hill (*Bull. Mus. Harvard*, Vol. 34, 1899) says that at the end of the Cretaceous and the beginning of the Eocene there was an extensive continental period, but that there was a subsidence at the end of the Eocene and in the Oligocene, and then again an uplift at the end of the Oligocene and in the Miocene. The latter is just the opposite movement from what is known for Cuba. It is quite likely that a different fate is to be assumed for the different islands, and it seems that Spencer's idea of contemporaneous subsidence or elevation of the whole region between North and South America is entirely wrong; the orogenetic movements and the changes of level connected with them were, after the first great subsidence of the Caribbean basin, more or less local and affected only limited parts, so that at the same time we may have had opposite movements in different sections of this region.



northern parts of South America (Archiguiana) once formed, during Mesozoic times, a part separated from the rest of South America, which, however, continued eastward across the Atlantic Ocean connecting with Africa. Fernando Noronha and St. Helena are remnants of this land-bridge, which he calls by the name of *Arch-helenis*. This connection was destroyed, according to von Ihering, in the Eocene, or, at any rate, not later than in the Oligocene.

To the numerous instances quoted by von Ihering in support of his theory the distribution of the family of the *Potamonidæ* adds another one, and the fact that two different subfamilies are found in the Old and the New Worlds, and that the affinities of the American forms with those of Africa and Asia are somewhat obscure, indicates that the connection of both is to be regarded as an old one and that it has been severed long ago. Therefore its existence in Mesozoic times and destruction in the beginning of the Tertiary, as maintained by von Ihering, has much in its favor.

Taking up the geological side of this question, we first have the broad Jurassic connection between Africa and South America assumed by Neumayr (1890). According to this author, and also according to Suess (1888, p. 677 ff), the whole of the southern Atlantic Ocean did not exist neither during the Jurassic nor during the older Cretaceous (Neumayr, *l. c.*, p. 376), since no traces of deposits belonging to these periods are found in West Africa or on the eastern shores of South America. It was not until the beginning of the Upper Cretaceous that sea washed the eastern parts of Brazil (*l. c.*, p. 389). But the connection of both continents persisted even then, although in a limited degree, and disappeared entirely as late as after the beginning of the Tertiary (*l. c.*, p. 397). Its last remnant (*l. c.*, p. 493) was formed by a chain of islands which extended in the Oligocene from tropical Africa to South America and the West Indies.

This view, however, is not accepted by Koken. In his map (1893, pl. 1) the Cretaceous continents of South America and Africa are absolutely separated in the earlier as well as in the later part of this period, and the Atlantic coast lines of both generally agree with the present ones. In the older Tertiary Koken (pl. 2) draws an island chain (Brazilo-Ethiopian islands) from the West Indies to Africa.

As far as it refers to the Cretaceous period, Koken seems to be mistaken. Although formerly it was supposed that Lower Creta-

ceous deposits are found in West Africa, it was soon recognized<sup>1</sup> that the respective beds are younger, and are certainly not older, than the Middle Cretaceous (in Cameroon); and especially Kossmat (1895) has demonstrated that the Cretaceous beds of West Africa (Angola, Elobi Islands, etc.) belong to the Middle and possibly the Upper Cretaceous (Cenomanian and Lower Senonian), and that they unmistakably possess a South Indian character, being connected probably around the Cape of Good Hope with the Indian Ocean. According to Kossmat, also the Brazilian Upper Cretaceous deposits in Sergipe, Pernambuco, etc.,<sup>2</sup> are of the South Indian type. Farther north, on the coasts of Morocco and Algiers, typical Mediterranean Cretaceous beds are present. The uppermost Cretaceous beds of Angola, however, are said to exhibit traces of the influence of the Mediterranean province (Kossmat, p. 465).

According to these facts we are to form the following idea as to the destruction of the old Brazilo-Ethiopian continent: It existed in its full development during the Jurassic and in the beginning of the Cretaceous time, being the western remnant of the old Paleozoic Gondwana Land, and probably it had the extension assigned to it by Neumayr—that is to say, it connected Africa with the northern as well as with the southern parts (Brazil) of South America. In the middle of the Cretaceous time the southern Atlantic Ocean was formed and the sea extended from the south (connected around the Cape of Good Hope with the Indian Ocean) toward the equator. About the same time, or rather a little later (in the Upper Cretaceous), a branch of the new South Atlantic extended into what is now the valley of the Amazonas river, separating the southern part of the Brazilian mass from the northern (Guiana) (compare below). *But Guiana remained connected with Africa*

<sup>1</sup> See Koenen, A. von, in *Abh. Ges. Wiss. Goettingen*, Ser. 2, Vol. 1, 1897, 1898.

<sup>2</sup> Described by White (*Arch. Mus. Rio Janeiro*, Vol. 7, 1888). Although some of these beds (marine beds in Sergipe and Parahyba) are without any doubt Upper Cretaceous, Branner (*Canadian Meeting Americ. Instit. Min. Engin.*, 1900, p. 17 f., and *Bull. Geol. Soc. America*, Vol. 13, 1902) has lately demonstrated that other marine sediments in Sergipe, Alagoas, Pernambuco, Parahyba, Rio Grande do Norte and Pará belong to the Eocene Tertiary (1902, pp. 47, 64, 85, 91, 96), and also that the freshwater deposits of the Bahia basin are probably Eocene (1900, p. 18).

and this restricted land-bridge going across the middle part of the Atlantic existed probably during the rest of the Cretaceous time and was not destroyed until the beginning of the Tertiary, a chain of islands remaining as late as the Oligocene.

This means, with respect to our freshwater crabs, *that their age goes back at least to the Upper Cretaceous*. During this period the last remnant of the continental connection between Africa and Guiana still existed, and the absence of *Potamonidæ* in South America south of the Amazonas valley further substantiates this assumption, that these crabs did not reach South America prior to the Upper Cretaceous, when the main part of Brazil also took part in this old continental connection. Aside from this fact, we have the consideration that it is not very likely that the age of the freshwater crabs goes far back in Cretaceous times. Although we have no definite information as to the latter point, we may say, from a morphological standpoint, that the *Potamonidæ* represent a peculiarly specialized side branch of primitive *Cyclometopa*. *Cyclometopa* existed in the beginning of the Cretaceous, but were rare. Thus an Upper Cretaceous age of the *Potamonidæ* is admissible.

The subsequent fate of the *Potamonidæ* in South and Central America, after they immigrated (or originated) in these parts in the later Cretaceous, will be discussed in the next chapter.

#### 8. THE MUTUAL RELATIONS OF NORTH, CENTRAL AND SOUTH AMERICA.

Aside from the peculiarities in the distribution of the freshwater Decapods of America, discussed above, there are several other features which need explanation. They are the following (see pp. 295, 296, 309):

1. The remarkable restriction of the genus *Potamobius* to the western parts of North America, while *Cambarus* is found in the east and south (Mexico).
2. The southern limit of the range of *Cambarus*.
3. The distribution of the *Potamocarcininae* over the West Indies, Central America and the northern parts of South America; their presence in the mountains of Ecuador and Peru and their absence in Brazil south of the Amazonas.
4. The peculiar shape of the areas of *Parastacus* and *Æglea*, which are almost identical, and extend, in the subtropical and tem-

perate parts of South America, from the Pacific to the Atlantic Ocean, but do not extend into the tropical parts.

In order to arrive at an understanding of these points it will be necessary to investigate the history of the origin and the mutual relations of North, Central and South America. It is generally conceded that these three parts have undergone various changes, but as regards the details there is much discussion and erroneous ideas prevail. It will hardly be possible in the following to give satisfactory answers to all of these questions, but we shall endeavor to collect all that is known as relating to the geological history, and we shall thus try to get an idea of the most prominent features of the history of the origin of the Americas.<sup>1</sup>

That America consists of three masses differing tectonically is well known. The nucleus of *North America* is formed by an old northern and eastern mass—the “Canadian shield” and the folded ranges to the south of it. The parts to the west of these were subject to various oscillations during Paleozoic and Mesozoic times, and finally the elevation of the chain of the Rocky Mountains, running in a north-southerly direction, resulted in the present configuration of North America.

*Central America* (including the northern coast of South America) consisted in older times of a system of old ranges with east-westerly strike, forming probably an old Paleozoic and Mesozoic continent (Antillean continent), which was destroyed at the end of the Mesozoic time. Since then Central America and the West Indies are composed only of the remnants of this continent, which in turn have undergone various changes.

*South America* consisted formerly of the old Brazilian plateau, which probably was part of old Gondwana Land (Australia, Africa, South America). The high mountain chains of the Cordilleras in the west did not exist for a long time, and this region was covered by sea probably up to near the end of the Mesozoic time. The elevation of the Cordilleras began at the end of the Cretaceous and continued during the Tertiary.

The present connection of the three Americas did not always

<sup>1</sup> We shall disregard all those questions which are not connected with and illustrated by the distribution of the freshwater Decapods—for instance, the supposed former connection of North and Northeast America with Europe.



exist, and was not brought about until the mutual relations had gone through various and entirely different stages.

*a. North America.*

If we want to get an idea of the configuration of North America during Mesozoic times, we have to consult in the first line Neumayr's well-known map (1890). According to this, in the Jurassic, the northern and eastern parts of North America formed a continental mass, which extended well to the west (Utah peninsula), while the northwest was covered by the sea that separated America from Northeastern Asia. At the same time this continent (Nearctic) was bounded by sea to the south, Mexico and the West Indies being submerged.<sup>1</sup> This representation, however, needs correction, chiefly as regards the West Indies, as we have seen above.

Differing but little from the view taken by Neumayr is that of Koken (1893, pl. 1) with respect to the Lower Cretaceous period; but here the land extends considerably to the northwest and includes parts of Mexico, a conception which is also to be modified, as we shall presently see.

The general history of North America during the Cretaceous period is best represented by Dana (1895, pp. 813, 874, 881). According to him, Western North America was largely land during the Lower Cretaceous and continuous with the rest. In the Upper Cretaceous, however, chiefly in its earlier part, a central depression became evident, which extended from the south (Gulf of Mexico) northward and possibly reached the Arctic Ocean, dividing the continent into an eastern and a western half. The western half, as we have seen above (p. 318), became connected across Bering Sea with Asia at about this time.<sup>2</sup> At the end of the Cretaceous (Laramie) and in the beginning of the Tertiary an extended elevation began, which culminated in the formation of the Rocky Mountains, and by this process the interior Cretaceous sea became land again, which resulted in the reconnection of Western and Eastern North America. But, although there was a geographical union, Eastern and Western North America remained separated bionomi-

<sup>1</sup> Compare, also, Logan, W. N., in *Journ. of Geology*, Vol. 8, 1900, but here the Jurassic ocean of the Northwest is considerably reduced in size and represented only by a shallow bay.

<sup>2</sup> Temporarily the Cretaceous sea of the interior was connected in British Columbia with the Pacific (see Kossmat, 1895, p. 474).

cally, the Upper Cretaceous sea barrier being replaced by a barrier formed by the Rocky Mountains.<sup>1</sup>

Looking now toward Mexico and its continuation southward, we shall refer in the first place to the papers of Hill (1893 and 1898). The history of Mexico in Pre-Cretaceous times is very obscure. Possibly it was covered by sea, as is also assumed by Neumayr, in the Jurassic, at least in part (Hill, 1898). But it seems to be well established that in the Lower Cretaceous (Hill, 1893) almost all of Mexico was submerged from the Atlantic to the Pacific side. This Lower Cretaceous sea was limited on the north by the southern coast of the North American continent, which extended from the old Appalachian region across the present Indian Territory and New Mexico to the Mexican province of Sonora.<sup>2</sup>

In the middle of the Cretaceous period (at the end of the Comanche series, Gault) a large part of Mexico became land, forming a southern continuation of the western part of North America, which was separated in the Upper Cretaceous from the eastern, and which therefore extended from British Columbia<sup>3</sup> to the Isthmus of Tehuantepec. This strip of land formed during this period a very important barrier, separating the marine faunas of the Pacific and Atlantic Oceans. While both faunas were more or less connected during the Lower Cretaceous across Mexico, they became separated later and never again communicated in this region.

The Isthmus of Tehuantepec consists, according to Spencer,<sup>4</sup> of the identical Lower Cretaceous deposits found in Mexico, and, further, according to Sapper,<sup>5</sup> Cretaceous rocks are found in the

<sup>1</sup> This barrier was probably emphasized by the development of desert conditions in and at the foot of this mountain range. Compare Scott, W. B., *An Introduction to Geology*, 1897, p. 500: "Probably the upheavals at the end of the Bridger and at the end of the Eocene had made the climate much drier by cutting off the moisture-laden winds."

<sup>2</sup> In 1898 (pp. 243 and 259) Hill qualifies his views, and says that it is doubtful whether the whole country (Mexico) was entirely submerged at any one time during this period. He thinks it was a mere shifting of the barrier between the Atlantic and Pacific. Compare, also, Stanton, T. W., in *Journ. of Geology*, Vol. 3, 1895, p. 861.

<sup>3</sup> And these parts must have been connected, as we have seen above, with Northeastern Asia.

<sup>4</sup> *Bull. Geolog. Soc. America*, Vol. 9, 1897.

<sup>5</sup> *Boll. Instit. Geol., Mexico*, Vol. 3, 1896.

Mexican State of Chiapas, which adjoins Guatemala. As regards Guatemala, we know that here old rocks appear which belong to the system of the Antillean continent (see above, p. 342). Thus we have reason to assume that, while Mexico was covered by the Lower Cretaceous seas which separated North and Central America, this whole region became land at about the middle of the Cretaceous, thus effecting a connection of Western North America with Central America (Guatemala) or with the old Antillean continent. This seems to be also the view of Hill, and he likewise believes that this connection was never subsequently interrupted.<sup>1</sup>

The result of the foregoing discussion is that during the Jurassic, and especially during the Lower Cretaceous, North America formed a unit, which was separated from Asia and which was also circumscribed by a shore line in the south, being disconnected from Central America. In the middle part of the Cretaceous Mexico was elevated, and this new-formed land connected the western part of North America with the Antillean continent. At about the same time a connection of Western North America with Northeastern Asia was established (by way of Bering Sea), and the Mexican Gulf extended northward, separating Western from Eastern North America.

*Thus we have, in the Upper Cretaceous, a strip of land extending from Northeastern Asia over Bering Sea and over the western side of North America to Mexico and the Antillean continent. Eastern North America was separated from this strip.*

*In the beginning of the Tertiary Eastern North America became reunited to this western section.*

*At the end of the Tertiary the Beringian connection with Asia was interrupted (see above, p. 317).*

This would lead us for our Crustaceans to the following conclusions: We have seen above (p. 319) that at any time, beginning in the Upper Cretaceous, *Potamobius* may have invaded the western parts of North America. This is again supported by the preceding

<sup>1</sup> See Hill, 1893, p. 323. Spencer (1897) assumes that there was a reestablishment of the connection of the Atlantic and Pacific Oceans across the Isthmus of Tehuantepec in late Tertiary times. The evidence for it, however, is entirely insufficient. The gravels found on the passes of the isthmus are of no value, since their marine character has not been demonstrated. Compare, also, Hill, 1898, p. 262, footnote.

considerations; in so far as it is confirmed that *Potamobius* cannot have been present in North America during the Lower Cretaceous, otherwise the remarkable restriction to the west would be inexplicable. But the genus must have immigrated during the Upper Cretaceous, since fossil remains of *Potamobiidae*<sup>1</sup> are known from the Eocene of North America. This latter fact, therefore, narrows down the time of immigration to more definite limits (those of the Upper Cretaceous), and at the same time explains its restriction to the west. During this period the western parts of the country were separated from the eastern by sea. At the same time there was a possibility for the crayfishes to reach Mexico, and it is easily understood that *Potamobius* then sent a branch southward; which subsequently developed on the Mexican plateau into *Cambarus*. After this, in the beginning of the Tertiary, *Cambarus* had a chance to migrate by way of Texas into Eastern North America, where it reaches its culmination in the present time.

The morphological differentiation of *Cambarus* from *Potamobius* probably took place in the beginning of the Tertiary, after the ranges of these genera had become separated. This separation is apparently due to a climatic change in the region between Mexico and central California, where desert conditions developed. This desert climate is not so pronounced on the eastern side of the continent, near the Atlantic coast in Texas, and, consequently, the area of *Cambarus* is not here interrupted between Mexico and the United States. A subsequent connection of the ranges of *Potamobius* and *Cambarus* in the interior of North America (in the region of the Rocky Mountains and the plains adjacent to their eastern slope) was impossible on account of the topographic and climatic barrier existing there in Tertiary times, which has been mentioned above (p. 354). The Rocky Mountains themselves and the arid regions are not favorable for the freshwater crayfishes. Thus the areas of both genera remained separated, and only in one case a species (*P. gambeli*) has crossed the continental divide in the region of the Yellowstone National Park. This, however, is very likely due to the capturing of streams that originally belonged to the Pacific slope by the Yellowstone river.

*b. Central America.*

The tectonic unity of the old Archaic and Paleozoic rocks known

<sup>1</sup> *Cambarus primævus* of Packard, from the Eocene of Western Wyoming, which is, however, according to Faxon (1885, p. 155), rather a *Potamobius*.



from Guatemala to Venezuela is also emphasized by Hill (1898, p. 239 ff.), and he also thinks that, during Mesozoic times, a continuous continental mass may have existed here, which reached as far as Trinidad. We have seen above that the destruction of this continent was probably due, in the first place, to the formation of the Caribbean depression, at the end of the Cretaceous. This also agrees with Hill's view (1898, p. 260 f.) that during the whole of the Cretaceous, or at least during the larger part of it, the Atlantic and the Pacific Oceans were separated in the region of Central America—that is to say, that there was a land connection between the northern parts of Central America and northern South America. But, according to Hill, this connection is not identical with the present isthmian region, but was situated chiefly to the west of it.

We have nothing to say against a western extension of this Cretaceous land (which probably extended as far as the Galapagos Islands), but we believe that the isthmian region and the present Caribbean Sea also were land during this time; the main point is, that there was a connection between Guatemala, Honduras, Nicaragua, and the Greater Antilles on the one side, and northern Venezuela on the other.

These conditions changed considerably during the Tertiary. First, the Caribbean Sea was formed, and possibly it extended farther to the west and southwest than it does now. At least, parts of the present land-bridge, the Isthmus of Panama, were covered entirely by sea in the earlier Tertiary, and that this sea reached from the present Caribbean Sea across to the Pacific is beyond doubt. In the first line, the part through which the Panama canal is to be built is composed entirely of deposits that are not older than Eocene and Oligocene (Hill, 1898, p. 236), and this well agrees with the investigations of Douvillé,<sup>1</sup> and Bertrand and Zurcher:<sup>2</sup> the Old Tertiary sea (Eocene and Oligocene) must have here extended entirely across the isthmus, from the Atlantic to the Pacific.

The same seems to be true for the Nicaragua canal. According to Hayes,<sup>3</sup> there are no rocks along this route that are older than Tertiary, and the Tertiary deposits probably belong to the Eocene and Oligocene. The remarkable discovery has been made that

<sup>1</sup> *C. R. Soc. geolog. France*, 1898.

<sup>2</sup> Bertrand, M. et Zurcher, O. *Etude géologique sur l'Isthme de Panama*, 1899.

<sup>3</sup> Hayes, C. W., "Physiography and Geology of Region Adjacent to the Nicaragua Canal Route" (*Bull. Geol. Soc. America*, Vol. 10, 1899).

sediments on the Pacific side contain the same fossils as the corresponding ones on the Caribbean side, which is an important addition to Hill's observations.

Between these depressions of the isthmian region, filled out by older Tertiary deposits, there are Archaic rocks at various places; we know of such not only from Guatemala and Honduras, but also from northern Nicaragua (Hayes), Costa Rica (Hill, Hayes), and even farther east, beyond the Panama canal, in the Cordilleras of San Blas. Thus it seems that the present isthmus, from Nicaragua to Colombia, consisted during the older Tertiary of a series of islands separated by ocean straits.

According to the unanimous opinion of Hill, Hayes, Bertrand and Zucher and others, these straits (Nicaragua and Panama) became dry in the Middle Tertiary, *i.e.*, *in the Miocene, and, consequently, the connection of North and South America was then established.*

Although this Eocene and Oligocene communication of the oceans is admitted by Hill, he is inclined to minimize its importance. Moreover, he assumes (1898, p. 263) that to the southward and westward, toward the Pacific, a large land mass must have existed, from which the material of the marine deposits of the isthmus was derived, and, further, he believes that this land mass chiefly extended in a north-southerly direction, probably connecting North and South America. I think we do not need this land, and even if we accept its existence,<sup>1</sup> it hardly formed, in the earlier Tertiary, a connection of the Americas. Be that as it may, the insular elevations of the isthmus, and the masses of old rocks to the north of it, in Nicaragua, Guatemala, Honduras, and in the supposed connecting land with Jamaica and Cuba (see above, p. 347), were in our opinion sufficient to furnish material for those Old Tertiary sediments in the isthmian region.<sup>2</sup> On the other hand, any

<sup>1</sup> Since we need, as I most emphatically believe, a connection with Galapagos Islands; this subject, however, is outside of the present question.

<sup>2</sup> Hill himself (1898, p. 263) discusses the idea that the land to the north of the isthmus may have furnished the material, but dismisses it, since here "we are confronted by great depths." Now, in my opinion, great depths are no fundamental objection, and just in this case the character of the sea bottom in the region between Honduras, Jamaica, Cuba and Hayti indicates that important disturbances have occurred here, and, in the first place, the deep submarine rift valley, known as "Bartlett deep," may be of a very recent age.

land mass to the south and west of the isthmus cannot have formed an Old Tertiary barrier completely separating both oceans, since we need an interoceanic communication during this time, as we shall presently see.

Our opinion is, that during the Cretaceous there was a connection between northern Central America and northern South America, the Antillean continent still being more or less intact. At the beginning of the Tertiary, however, and after the formation of the Caribbean Sea, an oceanic connection existed between the Atlantic and Pacific in the isthmian region, and this communication existed up to the Miocene, separating North and South America. But afterward, beginning in the Miocene, the isthmus was elevated, reconnecting the separated chief remnants of the Antillean continent, and at the same time North and South America. The Atlantic and Pacific Oceans were separated, and never again communicated, either here or elsewhere.<sup>1</sup>

We here arrive at a result which differs considerably from von Ihering's ideas as to the relations of North and South America: von Ihering believes (1894, p. 405) that both continents were separated by Cretaceous sea, and that Central America was entirely submerged at this time; the origin of the Isthmian land-bridge is also placed by von Ihering in the Miocene.

For our Crustaceans, we are to draw from this the following conclusions:

The presence of *Potamocarcininae* in the present continental parts of the old Antillean continent, in Nicaragua, Guatemala (to which we must add the southern parts of Mexico), the isthmian region and Venezuela, is due to the Cretaceous connection of these parts; the presence of the genus *Epilobocera* in the Greater Antilles is due to the former connection of these islands with the mainland, and belongs to the same land period, or to the continuation of it in the earlier part of the Tertiary. After the separation of the Greater

<sup>1</sup> This idea well agrees with the character of the present Atlantic and Pacific marine littoral faunas in the Central American region. These faunistic facts are often incorrectly represented and understood, and Hill's argument against the importance of the interoceanic communication in older Tertiary times is based upon such a misunderstanding. I have studied this question chiefly with reference to the marine Decapod Crustaceans, and shall give below a correct representation of the actual conditions of the faunal relations of both oceans. See Appendix.

Antilles from the mainland, there was left on these islands an isolated stock of primitive freshwater crabs, now known under the name of *Epilobocera*. On the mainland, these primitive forms disappeared, or changed into what is now known as the genus *Potamocarcinus*, and although in the beginning of the Tertiary the continental range of this genus was much cut up, chiefly in the region of the isthmus, the different parts were reunited in the Miocene, forming a unit that extended from northern Central America to Trinidad and Guiana. This explains the uniform distribution of *Potamocarcinus* over this region. In the later Tertiary we had a second union of the Greater Antilles with northern Central America, which explains the immigration of identical species of *Potamocarcinus* from Mexico into Cuba and Hayti. The Lesser Antilles were probably connected in the later Tertiary with Venezuela, and a species of freshwater crabs reached them by this way.

*c. Relation of Venezuela to the rest of South America. The Orinoco Valley.*

The northern coast range of Venezuela belongs, as has been stated, to Central America. To the south, on the slope toward the Orinoco, it is fringed by extensively developed Cretaceous deposits, which are also known from Trinidad in a similar position. These deposits are said to belong to the Lower Cretaceous (Suess, 1885, p. 688), and to extend westward far into Colombia. To the south of this zone, in Venezuela, there are (Suess, *ibid.*) younger Tertiary marine beds, which, in part, enter this region through a depression extending southward from the Bay of Barcelona on the northern coast of Venezuela.

This would indicate that during the Lower Cretaceous, the old Antillean continent was bounded on the south by sea (see above, p. 343), which separated it from the old granitic masses of Guiana. The apparent lack of Upper Cretaceous deposits, with the exception of a small region of western Venezuela, points to the assumption that at the end of the Mesozoic time (Upper Cretaceous) both regions were connected. Then again, in the later Tertiary, they were separated, at least in part, by sea that entered into the Orinoco valley (Suess, 1888, p. 161).

The Lower Cretaceous sea not only separated Venezuela and Guiana, but apparently continued westward, into Colombia, Ecuador and Peru. Indeed, there are in the western chain of the



Cordilleras in Peru and Bolivia many exposures of old (Archaic and Paleozoic) rocks; but the fact that in this region (from Colombia to Bolivia) Lower Cretaceous of the Mediterranean type has been discovered right in the Cordilleras,<sup>1</sup> renders it possible that those older rocks were originally covered by Mesozoic deposits, which were removed subsequently by erosion; and this is also the view of Suess (1885, p. 684, and 1888, p. 683), since he takes it for granted that the Cretaceous beds of the Upper Amazonas (and Orinoco) valley once continued across the whole continent to the Pacific Ocean.

Thus there would result, in Lower Cretaceous times, a complete separation of Central from South America by a sea, which extended from the region of the mouth of the Orinoco westward to Ecuador and Peru, *connecting the Atlantic and Pacific Oceans: in the Upper Cretaceous, however, Guiana was united with Venezuela.*

The *Potamocarininæ*, which, as we have seen above (p. 351), arrived in Guiana in the Upper Cretaceous (by way of the connection with Africa), found at this same time a land connection with the northern parts of Venezuela, and generally with the Antillean continent, and this explains their general distribution over Central America and the West Indian region, as set forth above (p. 308), and the origin of this distribution consequently falls in the *Upper Cretaceous*.

#### *d. South America.*

The separation and isolation of South America from Central, resp. North America during Mesozoic times as well as in the beginning of the Tertiary, forms the fundamental idea of von Ihering's Archiplata and Archhelenis theory (1891). But, according to him, the line of separation was situated in the present Amazonas valley, and existed during the Jurassic, Cretaceous and the Eocene; in the Oligocene the elevation of the Cordilleras began, and Archiplata (the southern part) was united with Archiguiana (Guiana and Venezuela), and it was not until the beginning of the second half of the Tertiary (Miocene) that these latter parts became united with North America by the formation of the Isthmus of Panama.

We can accept this view only in part, since the very important

<sup>1</sup> Hyatt, A., in *Proc. Boston Soc. Nat. Hist.*, Vol. 17, 1875, p. 365 ff.; Steimann, in *N. Jahrb. Mineral., etc.*, 1881, 2 p. 130 ff., 1882, 1 p. 166 ff., and Gerhardt, *ibid.*, Beil., Bd. 11, 1897.

interoceanic connection through the Orinoco valley, discussed above, is not taken account of, and since, as we shall see presently, the relations between Guiana and Brazil and between Guiana and Venezuela are much more complex than v. Ihering assumes.

Considering the tectonic configuration of South America, we are to mention, in the first place, that the whole eastern part is formed by the so-called *Brazilian mass* (Suess, 1885, p. 655 ff.): this is an old Archaic-Paleozoic plateau, which was possibly connected, from very early times up to the Lower Cretaceous (see p. 350), with Africa. Part of this mass is formed by the mountains of Guiana (Suess, 1885, p. 658), and the present valley of the Amazonas is a symmetrical syncline within the old plateau, in the centre of which are Carboniferous beds and, on top of the latter, Upper Cretaceous deposits. Thus the Amazonas valley was apparently land during most of the Mesozoic time, and Guiana was connected with Brazil; but in the Upper Cretaceous it was a wide sea, the northern and southern shores of which were formed by Paleozoic rocks (Suess, 1885, p. 660). This sea extended from the Atlantic westward into the region of the Upper Mara  n, in the Cordilleras, and probably connected with the Pacific Ocean (Suess, 1888, p. 683), which is very likely, since the western shore of the old Brazilian mass hardly extended to the eastern foothills of the Cordilleras (in a certain region, the present river Madeira marks the western boundary), and since it is quite sure that the Cordilleras were sea during the Jurassic as well as the larger part of the Cretaceous. This results in an Upper Cretaceous interoceanic connection between the southern Atlantic and the Pacific, which was situated about where the Amazonas valley now is. *This Upper Cretaceous strait agrees with the sea that separated von Ihering's Archiplata and Archiguiana*, but it is well to emphasize the fact that it is restricted, as a separating *strait*, to the *Upper Cretaceous* period: during previous times, especially the Jurassic and Lower Cretaceous, it did not exist at all, and later it was changed into a bay, as we shall see below. The interoceanic connection during the earlier Cretaceous was not situated here, but went by way of the Orinoco valley (see above, p. 360). The directions of both straits converge to the westward, and it is possible that they actually met, if they co  existed at any time: but generally, we are to maintain *that the separation of Central and South America during the Lower Cretaceous was effected by the Orinoco Strait, and that at this time Guiana was*

*united with Brazil, to which it belongs tectonically, while, in the Upper Cretaceous, Guiana was united with Central America, and was separated from Brazil by the transgression of the Atlantic Ocean in the Amazonas valley.*

This latter strait thus formed a continuation of the South Atlantic Ocean, which came into existence, as we have seen above (p. 350), at about the middle of the Cretaceous.

The Upper Cretaceous conditions were generally preserved in this region during the beginning of the Tertiary, and the Eocene and Oligocene sea extended, in the Amazonas transgression, far to the west (brackish Oligocene deposits are known near Pebas, Peru). But during this time (older Tertiary), the elevation of the Cordilleras must have become evident<sup>1</sup> in the western parts of this interoceanic connection, since older Tertiary deposits are wanting in this region. Thus those parts which now comprise Colombia, Ecuador, Peru and Bolivia became land, and the Amazonas Strait was shut off from the Pacific Ocean, being transformed into a deep bay, which occupied the Amazonas valley as far as the foothills of this new elevation (Cordilleras). Therefore, this interoceanic connection was interrupted in the beginning of the Tertiary, the main part of South America, or the old "Archiplatea" of von Ihering, becoming united with northern South America (Venezuela and Guiana). But we have seen above (p. 344) that at the same time (earlier Tertiary or uppermost Cretaceous) another interoceanic connection had formed in the isthmian region, and this replaced the Amazonas connection of the Upper Cretaceous era.

The old connection of the Brazilian mass with Africa continued in part as we have seen (p. 350) during the Upper Cretaceous, for its northern portion, Guiana. That is to say, an intermigration of the faunas of Guiana and Africa was yet possible in the Upper Cretaceous. The fact that during this time (and in the beginning of the Tertiary) a strait or bay extended along the region of the Amazonas river as far as the Pacific Ocean (or as far as the Cordilleras), furnishes the explanation for the zoogeographical fact that animals immigrating from Africa into Guiana during the Upper Cretaceous could reach Central America and the West Indies, but not those parts of Brazil which are to the south of this old Amazonas Strait: this seems to apply to our *Potamonidæ*, and

<sup>1</sup> The first signs of an elevation belong to the Upper Cretaceous.

explains their general absence south of the Amazonas. The extension of the range of these freshwater crabs into Colombia, Ecuador and Peru was not obstructed during the older Tertiary, since during this time these parts became land and were connected with Venezuela.

Regarding the extension of the old Brazilian mass (Archiplata) to the south, we know that the old Archaic, Paleozoic and Old-Mesozoic rocks continue in southern Bolivia and northern Argentina, into the eastern Cordilleras (Suess, 1885, p. 661); in Argentina, these rocks prevail in the northern parts: they are also found in the Pampean Sierras,<sup>1</sup> but do not seem to extend southward beyond the province of Buenos Ayres (Suess, 1885, p. 664). To the south of these parts the whole of Patagonia was apparently covered by the Cretaceous sea (Suess, 1888, p. 683, and above, p. 338). The Brazilian continent was also surrounded in the west by Jurassic and Cretaceous sea, as is demonstrated by the presence of the respective deposits in the region of the Chilian-Argentinian Cordilleras (see p. 338). As we have seen above (*ibid.*), it is very probable that during the Jurassic and a larger part of the Cretaceous era, the Brazilian mass was separated by this sea, which occupied present Patagonia and the site of the Cordilleras, from another continental mass lying to the west, southwest and south of it, which was formed by the present Chilian coast range and its southern continuation, which belonged, at least during the Cretaceous, to the Antarctic continent. At the end of the Cretaceous a land period began in these regions which culminated in the Eocene, and which effected a connection of the old Antarctica with Archiplata, chiefly in the region of the Chilian-Argentinian Cordilleras. This connection made possible the immigration of *Parastacus* into the southern parts of Archiplata (Argentina, Uruguay, southern Brazil), and it has remained up to the present time, although parts of Patagonia were again submerged during the course of the Tertiary.

The results obtained in the foregoing concerning the history of the American continent may be summed up as follows.

1. America originally consists of *three parts*: *North America* (its nucleus being in the East), the *Antillean continent* (comprising the West Indies, Central America and the northern coast of Venezuela) and the old *Brazilian mass* (Archiplata). Also a *fourth part* enters

<sup>1</sup> Valentin, J., *Bosquejo geologico de la Argentina*, 1898.



the present boundaries of South America, which is formed by the *Chilian-Fuegian coast range*, once a *part of Antarctica*.

2. *North America* was separated during the *Lower Cretaceous* from Central America. During the *Upper Cretaceous* it was divided into an eastern and a western portion; the western was definitively connected at this time with Central America. In the beginning of the *Tertiary* the eastern portion was reunited with the western, and thus the whole of North America, from the Arctic Ocean to the Gulf of Mexico and the Caribbean Sea, became a unit.

3. *Central America* existed as a continental mass up to the end of the *Cretaceous*. Being originally separated from North America, it became united with it in the *Upper Cretaceous*. By the formation of the Caribbean Sea it was broken up and consisted, in the *beginning of the Tertiary*, of two main parts: a *northern*, belonging to North America, and a *southern*, which became united with South America, then undergoing the process of construction. Both parts were separated by the Old Tertiary interoceanic connections at Panama and Nicaragua.

The *southern part* of Central America was originally (Lower Cretaceous) bounded on the south by sea, which occupied the region from the Orinoco valley westward. In the *Upper Cretaceous* Guiana was connected with Venezuela, and thus Central America was connected also with Africa. To the south of these parts was the Upper Cretaceous interoceanic connection of the Amazonas valley. In the *beginning of the Tertiary*, what was left of Central America in the south (Venezuela and Guiana) was united with the Brazilian mass by the beginning of the upheaval of the Cordilleras, by which parts of Colombia, Ecuador and Peru became land.

In the *middle of the Tertiary* (Miocene) the interoceanic connection in the isthmian region became land, and thus North America and the northern remnants of Central America were united with the southern remnants of Central America and South America.

4. *South America* consisted in the beginning (Jurassic and Lower Cretaceous) of the Brazilian mass (Archiplata), which included Guiana, and a smaller part which is perhaps of Cretaceous age, represented now by the Chilian coast range. Archiplata was connected with Africa up to the middle of the Cretaceous. In the *Upper Cretaceous*, Guiana was separated from Brazil by the interoceanic connection of the Amazonas valley and Archiplata became an island. At the *end of the Cretaceous*, and chiefly during the

*Eocene*, Archiplata became united with the Chilian coast range by the elevation of the Cordilleras, and it was thus connected with Antarctica. And, further, in the *beginning of the Tertiary*, Archiplata connected, by way of Peru and Ecuador, with Central America. This resulted in the final formation of South America (in its rough outlines) which, however, was still in communication with Antarctica. Finally, in the *middle of the Tertiary*, South America was united with North America (in the isthmian region) and was severed from Antarctica, and this represents the chief features of the present conditions.

We have seen that during the geological development of the Americas *interoceanic connections*, which were directed east-westerly, and united the waters of the Atlantic and Pacific Oceans, have repeatedly played a part. These connections being extremely important for marine zoogeography, have often been referred to by various authors, but have generally been misunderstood, the value of a determination of the exact time of their existence being neglected. So it will be worth while here to put them together by themselves.

*Interoceanic connections of the Atlantic and Pacific Oceans.*

1. In the *Lower Cretaceous* there were *two* connections: *a. across Mexico*, and *b. through the Orinoco valley*. Both probably united the marine fauna of the Mediterranean province with that of the (Indo-) Pacific.

2. In the *Upper Cretaceous* we have the connection through the *Amazonas valley*. This united the South Atlantic fauna, which, in this period, formed part of the Indo-Pacific, with the identical fauna of the eastern Pacific.

3. In the *Older Tertiary* there existed the *Panamic connection*, which united the fauna of the Atlantic, the chief element of which is Mediterranean, with that of the Indo-Pacific.

4. In the *Later Tertiary* no interoceanic connection existed, the Atlantic and Pacific faunas being sharply separated. These conditions continued up to the present time.

It is impossible to say at present whether there were any transitions between these different stages. A coëxistence and union of the connections 1 and 2, at about the beginning of the Upper Cretaceous, is possible in the region of the Upper Orinoco and Upper

Amazonas. But we have no evidence for this, the Geology of the respective countries being too incompletely known.

#### 9. THE RELATIONS OF AFRICA TO THE REST OF THE WORLD.

We have seen (p. 303) that for the two main divisions of the range of the *Potamoninae* in the Old World Egypt and the Nile valley form an actual connection; but examining this more closely we find that this subfamily cannot have migrated along this route from Africa to India (or vice versa), but entered Egypt from two opposite directions, from the south (Central Africa) and the north (resp. northeast) over Persia, Mesopotamia and Syria.

The causes why this way was not open in former times have been briefly mentioned above (p. 333), and we shall here try to investigate the relations of Africa and Asia with respect chiefly to this northern connection. For this purpose we are to discuss also the northern boundaries of Africa with reference to Europe. This is the more important, since we have to consider the alleged fact that fossil forms of the *Potamoninae* have been found in Miocene freshwater deposits of Oeningen (Switzerland), Sigmaringen (Southern Germany) and Northern Italy.<sup>1</sup>

Very important for a study of these questions is the former existence of a *Central Mediterranean Sea*, as Neumayr calls it (1890, pp. 332, 333, and map p. 336), or the *Tethys* of Suess (1894). This ancient sea goes back to Paleozoic times and covered in Mesozoic times the whole of Middle and Southern Europe, the present Mediterranean Sea, Northern Africa and extended eastward over Asia Minor, Syria, the Caucasus Mountains and Mesopotamia as far as Northern India. In the east a large bay extended southward along the East African coast, which separated the Indo-Madagassian peninsula (Lemuria) from Africa. In a westerly direction the Tethys was broadly connected with the Atlantic Ocean, leaving only the island of Spain (Meseta) uncovered.

In these general outlines the Tethys existed in Jurassic as well as in Cretaceous times, thus completely circumscribing the African continent toward the north and northeast. Europe did not then exist at all as a continental mass and Africa was separated from the Sinic continent by an eastern continuation of the Tethys, the

<sup>1</sup> *Thelphusa speciosa* Mey. and *Th. quenstedti* Zitt., see Zittel, *Handbuch d. Paläontol.*, Vol. 2, 1885, p. 714. These forms have a remote resemblance to the subgenus *Potamonaula*, if they belong here at all.

*Strait of Bengal*.<sup>1</sup> The only connection of Africa during these times was with South America, the old Archiplata (Jurassic and Lower Cretaceous) and the old Archiguiana (Archhelenis, Upper Cretaceous). On the southern margin of the Tethys, as sketched above, there is a zone in the desert region of North Africa and Arabia, where Jurassic deposits are wanting and Cretaceous directly overlies Paleozoic beds. This indicates a farther extension of Africa northward in Jurassic times and a transgression of the sea southward in the Cretaceous (Neumayr, 1890, p. 386). The deposits of the Cretaceous sea can be traced very distinctly in a broad belt from Syria over Arabia, Persia, Afghanistan and Beluchistan to Northern India.

Also in the Older Tertiary (Neumayr, p. 480) the Central Mediterranean Sea reaches from the Atlantic Ocean to India, and it was not until after the end of the Oligocene that its unity was destroyed. In the beginning of the Miocene Western Asia became largely land, and thus a broad connection was established from Asia to Africa (India to Arabia), and at the same time from Asia to Europe, which was then forming (Neumayr, 1890, p. 501 f.).

In detail the processes in the northeastern part of Africa were the following: Arabia during Mesozoic and the greater part of Tertiary times was broadly connected with Africa. The Red Sea did not exist, according to the unanimous opinion of all writers (Neumayr, Suess, Gregory, Blankenhorn and others). The origin of the Red Sea falls late in Tertiary times, after the connection of Africa with India was long established, and thus, in the second half of the Tertiary, a regular exchange of the faunas of Africa and India could take place, for which we possess ample evidence.

The Red Sea is a rift valley, which is tectonically connected with the valley of the Jordan river in Palestine.<sup>2</sup> The most detailed investigations on this question have been published by Blankenhorn.<sup>3</sup> According to this author, the Mediterranean Sea (the western part of the old Tethys) in Miocene times sent a wide bay to the southeast, which extended as far as the southern end of the Gulf of Suez, which, of course, did not then exist, and the Nile

<sup>1</sup> Which, however, was temporarily interrupted during the Upper Cretaceous. See above, p. 330.

<sup>2</sup> See Gregory, J. W., in *Proc. Zool. Soc. London*, 1894, p. 165.

<sup>3</sup> Blankenhorn, M., in *Centralbl. f. Mineral., etc.*, 1900, p. 209 ff.



valley.<sup>1</sup> The latter and the Red Sea originated in the Pliocene. Into the Nile valley entered the Pliocene Mediterranean Sea. It then changed into a series of inland lakes, and finally, in the middle Diluvial time, it became a river valley. The depression of the Red Sea was occupied first (Pliocene) by inland lakes, and finally, toward the end of the Pliocene, by the Indian Ocean, which entered it from the south.<sup>2</sup> The present separation of Africa and Arabia (Asia), which is nearly complete, belongs, therefore, to a very recent date. In the later Tertiary Southern Asia and Africa were not distinguished zoogeographically, while in older times (Pre-Miocene) there was a complete separation of Africa (including Arabia) from the Sinic continent, and only during the second half of the Cretaceous was there a limited connection by way of Madagascar and the Indian peninsula.<sup>3</sup>

The old isolation of Africa was ended not only in these eastern parts during the Tertiary, but also in the northwest changes occurred which extended Africa and brought it into contact with Western Europe.

The Cretaceous sea covering Northwestern Africa was no doubt considerably reduced in the Tertiary. Indeed, there are Tertiary deposits in this region, and according to Suess (1888, p. 155), the Middle Tertiary sea probably also covered the Western Sahara. But about this time apparently a land connection was formed to the north toward the old Spanish Meseta. According to Bergeron,<sup>4</sup> the Algerian Sahara possesses deposits from the Senonian to the Pliocene, but these are bounded in the west by a Cretaceous mountain

<sup>1</sup> In the region of the Nile valley there was a river, but this was not the Nile, but came from the west out of the Libyan desert.

<sup>2</sup> An actual connection of the Red Sea and the Mediterranean Sea is very doubtful, but was possibly established for a short time in the beginning of Diluvial times, when the Mediterranean Sea became cold. The improbability of a connection of both seas is especially emphasized by Jousseume (*Ann. Sci. Nat.*, Ser. 7, Vol. 12, 1891). According to him, the Red Sea is Quarternary (Diluvial).

<sup>3</sup> The oceanic connection from the Gulf of Aden across the Sahara desert to the Atlantic (Senegambia), advanced by Jousseume (*l. c.*), has no geological support. It is founded upon an alleged similarity of the Mollusk faunas of both parts, which, however, needs closer investigation and might possibly find its explanation in the configuration of the Pre-Miocene Tethys, which reached from the Persian Gulf to the Mediterranean Sea and Atlantic Ocean.

<sup>4</sup> In *Mem. Soc. Ingen. civ. France*, 1897.

range running north-south. In Algeria we have, according to Lap-parent,<sup>1</sup> deposits of Cretaceous and Eocene age, but only traces of Oligocene, and thus we can place the upheaval of these parts at the end of the Eocene, and probably at this time the connection with Southwestern Europe began to develop. The mountain range along the northern coast of Algiers, as far as the Strait of Gibraltar, consists of rocks which (see Suess, 1883, p. 293 ff.) are also found in the so-called Betic Cordilleras (*ibid.*, p. 298) in Southern Spain, and the tectonic unity of these ranges of Algiers and Spain is especially emphasized by Suess, as well as their tectonic connection with the Apennines and the Alps. The origin of all these mountain chains was near the end of the first half of the Tertiary, about the Oligocene time.

But this connection of the northwestern parts of Africa and of Southern Spain with the rest of Africa did not constitute a complete union with Europe. We know that the central and northern region of Spain, the Iberian Meseta, is an old land, but that to the south and north of it, on the one side along the valley of the Guadalquivir river in Spain, on the other in the region of the Garonne river in France, connections of the Mediterranean Sea with the Atlantic Ocean existed. According to Suess (1885, p. 381; see also Neumayr, 1890, p. 516), in the valley of the Guadalquivir there are Tertiary deposits, reaching from the Atlantic to the Mediterranean Sea, which belong to the first and second Mediterranean stage—that is to say, to the Miocene—while deposits of the third Mediterranean stage (Pliocene) have not been found. Consequently this strait (Betic Strait) became dry at the end of the Miocene, and by this process the northern part of Spain was united with the southern and with Algiers and Africa.

The disappearance of this strait was the last step which resulted in a definitive connection of Africa with Europe, since the strait in the region of the Garonne river, in Southern France, became probably land a little earlier, namely, at the end of the Oligocene (see Suess, 1885, p. 382 ff., and Neumayr, 1890, p. 516).

But it is to be borne in mind that possibly the conditions were not so simple as has been represented above. According to Lap-parent (*l. c.*, pp. 1291 and 1313), the Betic Strait (*détroit bétic*, also called Andalusian connection) was dry during the Oligocene,

<sup>1</sup> *Traité de Géologie*, Vol. 2, 1893, p. 1291.

while sea again occupied it in the Miocene, and thus we would have a chance for the African fauna to reach Northern Spain as early as the Oligocene. This connection, however, scarcely amounted to a complete communication of Africa and Europe, since at that time the Oligocene strait to the north of the Iberian Meseta was still in existence, forming a barrier to the further advance of the African fauna. Thus, even under this assumption, a final connection of Africa and Europe was not established until the end of the Miocene, after the second obliteration of the Betic Strait. Subsequently the connection of both continents was again interrupted by the formation of the Strait of Gibraltar; but this belongs to very recent times.<sup>1</sup>

Another tectonic line goes from Northwestern Africa to Sicily and Italy, and is marked by the eastern continuation of the same mountain range that curves in the west from Africa into Southern Spain. This system belongs to Post-Oligocene times, and as a land-bridge apparently underwent repeated changes. Moreover, it is doubtful whether it existed at any time as a complete and solid bridge, but it is represented as such by Scharff (1895, maps pp. 465 and 470) for the Pliocene time,<sup>2</sup> while Neumayr (1890, Vol. I, p. 330), for the *Lower* Pliocene, gives only a series of islands.

From the above discussion we are to draw the conclusion that—aside from a connection with the Sinic continent during the Upper

<sup>1</sup> Kobelt, W. (*Studien zur Zoogeographie*—"2. Die Fauna der mediterranen Subregion," 1898), arrives at a different conclusion. According to him, the Mediterranean Sea was separated from the Atlantic Ocean in the *Older* Tertiary by a connection of Central Spain with the Atlas mountains (the Sierra Nevada or Betic Cordilleras did not then exist). The Miocene Tethys reached from India to Spain and Central France, but did not communicate with the Atlantic, the connection along the valley of the Guadalquivir being of Pliocene age.

This result is contrary, however, as we have seen, to what is known of the Geology of these parts. Just the opposite is the case. In the Older Tertiary the Tethys and the Atlantic were broadly connected, and in the Miocene they still communicated through the Andalusian or Betic Strait, as is positively shown by the presence of Miocene beds there. But in Pliocene times this strait was dry land.

<sup>2</sup> According to Scharff (in 1897, pp. 461 and 466), this bridge belongs to the *Upper* Pliocene and Glacial times. We shall become acquainted below with the evidence for its existence as an actually connecting bridge.

Cretaceous—Africa, for a very long time, was isolated from the rest of the Old World. After it had become disconnected from South America, at the beginning of the Tertiary, it was absolutely isolated, but soon during the course of the Tertiary it became united with Asia and the new continent of Europe. The most important stages in this process were that of the elevation of Western Asia, in the Miocene, and the elevation of the northwestern parts of Africa and southwestern parts of Europe at about the same time.

This has the following bearing upon the origin of the distribution of our freshwater Crustaceans: The African types of the subfamily *Potamoninae* (chiefly the subgenus *Potamonantes*) could not reach Europe before Miocene times, and, on the other hand, an immigration of the Asiatic types (subgenus *Potamon*) into Africa (and Europe) was also impossible before the Miocene and after the destruction of the Madagassian land-bridge in the earlier Eocene.

Whether the alleged fossil species of *Potamon* from the Miocene of Europe indicate this Miocene connection of Asia, Africa and Europe remains doubtful. The lack of African types in the Mediterranean region of the present time, as well as the general absence of a northerly and easterly advance of them (except in the Nile valley, where the immigration no doubt belongs to a very recent period), is opposed to the above assumption, and it is quite possible that these fossil forms do not belong to relations of the *Potamoninae*. It seems that the desert zone of the Sahara already existed in Miocene times, at least that it began to develop at the same time that Western Asia became land, since just this process furnished the conditions for the origin of an arid climate in North Africa and West Asia. On the other hand, we see that a species of the subgenus *Potamon*, belonging to the Indian fauna, advanced in a westerly direction across the new land areas formed in Miocene time, and that it reached by this route Northern Africa (Egypt and Algiers). But the distribution of this species (*Potamon fluviatile*) needs further explanation, since it is also found in certain parts of Europe, and we shall discuss this question in the next chapter.

#### 10. RELATIONS OF EUROPE TO ASIA.

In discussing the distribution of *Potamon fluviatile* in Southern Europe, just referred to, we are also to consider the presence of the genus *Potamobius* in Europe, the area of which is separated from that of the rest of the genus (in Northeast Asia and Northwest



America). The essential point in this respect is the investigation of the geological relation of Europe to Asia.

Europe did not exist as a continent—*i.e.*, as a continuous mass—from the beginning of the earth's history up to about the middle of the Tertiary. Indeed, there was a number of larger and smaller islands in the old Tethys, but they never were connected so as to assume continental shape. To the north, however, we had the large Scandinavian mass, which probably was connected over Greenland with North America, but we shall disregard this possible junction, since our present material, the Decapod Crustaceans, do not furnish additional facts which bear upon it.

The Tethys, as we have seen (p. 367), covered the whole region of the present Mediterranean Sea and extended over Western Asia, reaching, in the older Eocene, not only as far as the Indian Ocean, but in an easterly and northerly direction as far as the eastern side of the Kuen-Lun mountains and the Gobi desert.<sup>1</sup> Subsequently, in the Miocene, the western parts of Asia (from Asia Minor and Syria to India) became land (Neumayr, p. 501), and the Tethys was cut into a western (the present Mediterranean Sea) and an eastern section (forming part of the Indian Ocean). But during this time, and even afterward, the northern and northeastern parts of the old Tethys persisted. The Miocene Mediterranean Sea (Neumayr, 1890, p. 516) sent a strait from the basin of the Rhone river (France) through Switzerland into Austria, which there widened out into the Pannonian basin and in the Upper Miocene became a huge inland sea, the Sarmatian, which was cut off from its former western connection with the Mediterranean and reached from Austria over Southern Russia into the region of the Caspian and Aral Seas (Neumayr, p. 523). To the south of this sea the present Balkan Peninsula, the Ægean Sea and Asia Minor were largely land, but in Eastern Asia Minor a continuation of the Mediterranean Sea approached almost to the Black Sea. The region of the Caucasus mountains was probably sea up to Miocene

<sup>1</sup> In the Kuen-Lun mountains there are, according to Bogdanowitsch (*Geolog. Untersuch. im oestlichen Turkestan*, 1892, Russian. Review in *Neues Jahrb. f. Mineral.*, etc., 1895, Vol. 2, p. 110), Archaic and Paleozoic rocks and traces of Jurassic deposits (coal-bearing strata), and then again marine Cretaceous beds. Thus it seems that these mountains were land since beginning of the Mesozoic times and formed part of the Sinic continent. During the Cretaceous there was a temporary transgression of the sea.

times, as is shown by a continuous series of sediments lying upon Azoic rocks. Here<sup>1</sup> has been found Jurassic, Cretaceous, Eocene, Oligocene and Miocene. The latter deposits (Miocene) belong to the Sarmatian inland sea. Beginning with the Pontic stage, the sea recedes on the southern side of the Caucasus (freshwater deposits), while on the northern side marine deposits, belonging to the Ponto-Caspian Sea, continue. The latter disappear after the Glacial period.

The map, given by Neumayr, of the Eastern Mediterranean countries during the Lower Pliocene (1890, Vol. 1, p. 330, see also Vol. 2, p. 526) exhibits a much more extended development of land than at the present time. Especially striking is the direct connection of Asia Minor with the Balkan Peninsula and Central Europe. The corresponding map for the Later Pliocene, given by Scharff (1895, p. 465, and 1897, p. 461), indicates an additional land connection from Dalmatia over Southern Italy and Sicily to Algiers (see also 1895, p. 470, and 1897, p. 461), which is represented in Neumayr's map only by a series of islands.<sup>2</sup> Thus we obtain a continuous land connection from Asia Minor to North-western Africa, belonging to the Pliocene age.

In the Pleistocene (Glacial) time, according to Scharff (1897, map p. 466), this connection is still present.

In the northern parts of Europe we have no land connection in an easterly direction during the Cretaceous time. According to Koken (1893), however, North Asia was connected with Scandinavia in the *Upper* Cretaceous, forming part of a huge circumpolar Arctic continent; but the evidence for its existence seems to be very doubtful. For the Older Tertiary, Koken again indicates a separation of Northern Europe from Asia. In subsequent times, up to the Later Pliocene, the Sarmatian Sea covered the whole of Northeast Europe (Scharff, 1897, map p. 461), thus perpetuating the separation from Asia. During Glacial times this separation was maintained by the ice sheet covering Northern Russia and by the existence of the Aralo Caspian basin, and it was not until Interglacial times that a communication of Asia and Central

<sup>1</sup> See Fournier, in *Ann. Fac. Sci. Marseille*, Vol. 7, 1896.

<sup>2</sup> The *large* extension of the Mediterranean Sea to the south of Algiers over the Sahara desert in a westerly direction, as shown by Scharff's map (p. 470), is probably erroneous.

Europe was established north of the Aralo-Caspian basin over Southern Russia (Scharff, 1897, map p. 466).

The gradual origin of Europe, beginning with the formation of the chief mountain chains in the Oligocene, its connection first of the southern and central parts with Western Asia across the Balkan Peninsula (Miocene and Pliocene) and with Northern Africa over Spain (end of the Miocene), and subsequently the connection of the central and northern parts with Siberia (over Russia), by which processes Europe assumed the shape of a continent (part of Asia), have been largely used by previous authors for the explanation of the zoogeographical conditions of Europe.

Osborn (1900, p. 569) mentions a repeated immigration of Mammals into Europe and indicates the Upper Eocene, the Miocene and the Pliocene times as most important in this respect. But we must always bear in mind that during the Older Tertiary Europe was not a unit at all—in fact did not exist as a zoogeographical section. The Old Tertiary Mammalian faunas of Europe (chiefly in the Northwest, in France) probably belong to the British-Scandinavian mass, which was connected, as has been mentioned incidentally, with North America.<sup>1</sup> Then, in the Miocene, we have in Europe, which assumes a more consistent shape, a fauna of new character, the origin of which is to be sought in the East and Southeast (Asia), and possibly during this time the first African types reached Europe, either by the roundabout way over Western Asia or more directly over Algiers and Spain.

Kobelt (1897) also assumes an isolation of Europe at the beginning of the Tertiary, and discusses the immigration of an Indo-Chinese fauna from the East in Pliocene times, while the Nile valley formed a route by which freshwater animals immigrated from the South (Africa).<sup>2</sup>

The most detailed investigations on this question have been pub-

<sup>1</sup> As to this connection, which is not treated here, I refer the reader to Neumayr (1890, Vol. 2, pp. 497 and 504) and to Scott (*An Introduction to Geology*, 1897, p. 505).

<sup>2</sup> Contrary to this, Pilsbry (1894) is inclined to assume, for the *Helices*, a Cretaceous immigration from Southeastern Asia into Europe and Africa. But according to the present state of our knowledge, as set forth above, the history of the development of Africa and Europe, as well as of Asia, does not warrant this assumption. There was no possibility, on geological grounds, for the old Sinic fauna to reach Europe and Northern Africa before the Miocene.

lished by Scharff (1897). He distinguishes—aside from an Arctic migration—two main routes of immigration into Europe during the Later Tertiary period: 1, a *southern* one during Miocene and Pliocene, which was directed from Western Asia over Asia Minor, the Balkan Peninsula, Italy, Sicily, Algiers and Spain (and which apparently sent a branch from the Balkan Peninsula into Central Europe), and 2, a *Siberian* migration from Western Siberia through Southern Russia to Central Europe, which belongs to the Pleistocene (see map, *l. c.*, p. 466) and was impossible before this time (in Miocene and Pliocene), the Sarmatian and Ponto-Caspian Sea forming barriers.

Comparing our freshwater Decapods with the above, we see at the first glance that the present distribution of the European freshwater crab, *Potamon fluviatile*, unmistakably agrees with that land connection which began in the Miocene and culminated in the Pliocene and which extends from Asia Minor over the Balkan Peninsula to Italy, Sicily and Algiers. Even the minor features of it are traceable. *Potamon fluviatile* is found everywhere in Western Asia, in the Caucasus region and in the Crimea, but is missing in the rest of Southern Russia. This corresponds to the fact that the Crimea was connected in Pliocene times with the Caucasus and was not in communication with the rest of Russia (see Scharff, 1897, map p. 461). *Potamon fluviatile* is found in Asia Minor, Syria, on the island of Cyprus and in Egypt. All these parts were then connected. Along the tract of the land-bridge, from Asia Minor to Italy and Algiers, this crab has been everywhere found.<sup>1</sup> This relation of the supposed Pliocene land extension with the distribution of *Potamon fluviatile* is so close that there is no objection whatever to the assumption that the immigration of this species falls in the *Upper Pliocene*, when this land connection was fully developed, and not in the Lower Pliocene, when there was only a series of islands (see p. 374).

Turning now to the crayfishes of Europe, we see that the centre of the range of the group of *Potamobius astacus* (the Russian crayfishes) is just in that region which, during Miocene, Pliocene and

<sup>1</sup> That this species extended, in former times, farther to the north from the Balkan Peninsula is shown by the discovery of it in fossil state in diluvial calcareous tufa near Süttö, Com. Komarom, Hungary (see Loerenthey, E., *Nat. Hefte Ungar. Nat. Mus.*, 1898. Review in *Neues Jahrb. f. Mineral.*, etc., 1900, Vol. 2, p. 473).



the beginning of the Pleistocene, was covered by the Sarmatian and Ponto-Caspian Sea. This group consequently can only have reached these parts at a later period, namely, in Interglacial or Postglacial times, and its immigration no doubt corresponds to the Siberian of Scharff (*l. c.*, pp. 448 and 466). In regard to the other group formed by the two species, *P. pallipes* and *torrentium*, which occupy the South and West of Europe, we have to call attention to the important fact that this group is found not only in Southern and Western Europe, but also in England. Now we know that England was connected with the continent in Preglacial and even during Glacial times, and that this connection existed up to the beginning of the Siberian migration (Interglacial). It was interrupted later—according to Osborn (1900, p. 572), at about this time (Middle Pleistocene) and possibly even later.<sup>1</sup>

The fact that *Potamobius astacus* is found in France, but not in England, while *P. pallipes* passes over into the latter country, points to a difference in time of the immigration of either species. *P. pallipes* arrived in these parts before the end of the Glacial time, *P. astacus* at the end of it or even later. The latter consequently without doubt belongs to the Siberian migration, but rather to the later part of it. *P. pallipes* may belong to the earlier Interglacial part of the Siberian migration and have come from East and Central Europe; but it is also possible that it belongs to Scharff's southern migration and came from Asia Minor over the Balkan Peninsula. It is true, forms of the *pallipes* group have not been found in Asia Minor nor in Algiers, but it is not impossible that such may be discovered in these parts, or that they once existed there and have now disappeared. We shall see below why this latter assumption is admissible. The crayfishes in Asia Minor, Southern Italy and Algiers may have been exterminated by the freshwater crabs subsequently occupying these parts. Until this question is finally settled it is impossible to decide whether the group of *P. pallipes* has reached its present area by the southern route (Miocene-Pliocene) or by the route of the Siberian migration (end of the Pleistocene); but however that may be it arrived in Europe before the group of *P. astacus*.

The connection of the European crayfishes with the Sinic conti-

<sup>1</sup> Suess (1888, p. 528) thinks it possible that this happened in historic time or shortly before the beginning of it.

ment, where presumably their original home was located, is not yet established. It must necessarily have gone over Central Asia. Crayfishes of the European type are found eastward as far as Turkestan. It is doubtful whether crayfishes are absolutely lacking in the region between Turkestan and the Amur river. None are reported, but these parts are very poorly known. For the present I cannot imagine any reason for their disappearance in this region, in which they must have once existed, and therefore it is well to suspend judgment until these parts have been properly investigated.<sup>1</sup>

## SUMMARY OF RESULTS OF PART II.

### A. HISTORY OF THE CONTINENTS.

#### *a. Lower Cretaceous.* (See Fig. 5, p. 379.)

I. During the Lower Cretaceous there existed a *Sino-Australian continent*, comprising *eastern Asia*, the *Indo-Malaysian Archipelago* and *Australia*, and which was continued to *Antarctica*. We may retain for this continent the name SINO-AUSTRALIAN, although it is larger than that drawn by Neumayr for the Jurassic time. We are justified in doing this, since probably the Jurassic *Sino-Australia* also included Antarctica.

II. Besides, we have a *Nearctic continent*: this consists of the larger part of present *North America*, and extended probably across *Greenland* to the *Scandinavian mass* of North Europe. This continent also corresponds closely to Neumayr's NEARCTICA of Jurassic times, and consequently we have retained this name for it.

III. A third continent was formed by *Central America*, and we shall call this by the name ANTILLIA. Its remnants are now found in *Central America*, the *West Indian Islands* and *northern South America* (excluding Guiana). This continent is not given by Neumayr for the Jurassic, but probably existed then.

IV. A fourth continent was formed by the western portion of old

<sup>1</sup> A theory lately propounded by C. F. Wright (see *Science*, Vol. 16, Aug. 15, 1902, p. 262 f.) would go far toward an explanation of the causes leading to the destruction of the Central Asiatic crayfishes if properly supported. Wright believes that Northern and Central Asia was largely covered by water in recent geological time, but the evidence introduced for this is, in my opinion, entirely inappropriate. Of the five points mentioned by Wright two (Nos. 3 and 4) have no bearing at all upon this theory, and the value of the other three, especially of the fifth, is highly questionable.



FIG. 5. Distribution of land and water during the *Lower Cretaceous* period.

Gondwana Land. It comprises the *Brazilian mass* (including Guiana) and *tropical Africa* with the *Lemurian Peninsula* (Madagascar-India). This continent corresponds, generally, to Neumayr's Jurassic *Brazilo-Ethiopian* continent, but comprises a smaller part of South America (also, for Jurassic times, the section of South America that entered it, according to Neumayr, is too large). It agrees to a certain degree with what v. Ihering has called *Archhelenis*, although it is larger, and it may be permitted in this sense to modify the conception of ARCHHELENIS.

Thus in Lower Cretaceous times we have the following four continental masses: *Sino-Australia*, *Nearctica*, *Antillia*, *Archhelenis*, which were mutually isolated. Besides, there were smaller islands, chiefly in the region of present Europe.

b. *Upper Cretaceous*. (See Fig. 6, p. 381.)

The following changes took place:

*Sino-Australia* was divided into a *Sinic* (Asiatic) and an *Australian* part, the latter comprising Australia and Antarctica.

The *Sinic* section of Sino-Australia became united, across Bering Sea, with the *western part of Nearctica*.

The *western part of Nearctica* was separated from the *eastern*.

The *western part of Nearctica* became united with *Antillia*.

*Guiana* became united with *Antillia* and separated from the *Brazilian mass*.

*Brazil* became disconnected from *Africa*.

The *Lemurian bridge* was connected with the *Sinic continent*.

The result of this is:

I. *An irregular ring of land around the earth*, which, generally, encircles it in the direction of the equator, but curving far to the north in the region of the Pacific Ocean. This ring, beginning at the *Sinic land*, goes across *Bering Sea* to *western North America*, thence to *Antillia*, *Guiana*, *Africa* and the *Lemurian land-bridge*, which latter completes it by its union with the *Sinic land*. We may call this ring-shaped continent MESOZONIA.

Aside from Mesozonia we have, separated from it, the following continental masses:

II. UPPER CRETACEOUS NEARCTICA. Smaller than the Lower Cretaceous continent of the same name, since its western part is cut off and enters Mesozonia.



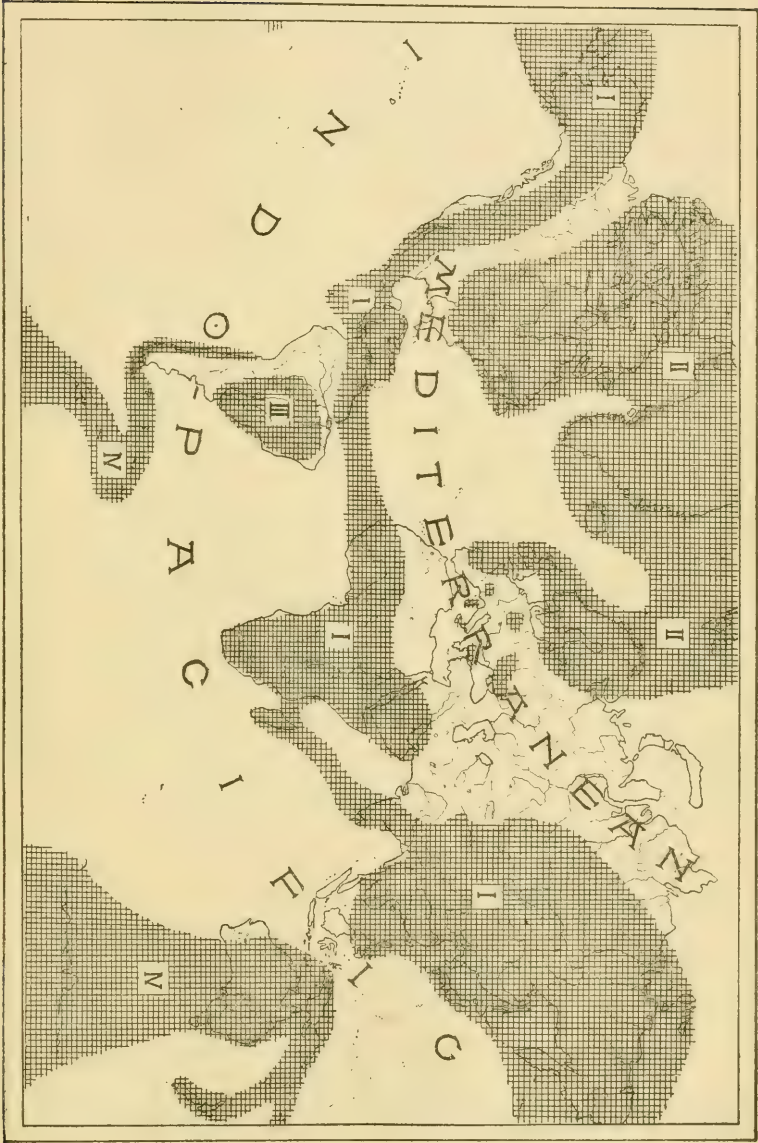


FIG. 6. Distribution of land and water during the *Upper Cretaceous* period.

III. ARCHIPLATA of von Ihering, comprising *Brazil*, south of the Amazonas, and *northern Argentina*.

IV. ARCHINOTIS, comprising *Australia* and *Antarctica*. As will be noticed, the term *Archinotis* (as used by von Ihering and others) does not exactly correspond to the meaning given to it here, but we think it convenient to define this term in this way, applying it only to the truly notal regions; aside from *Australia* and *Antarctica*, a part of *South America* belongs to Archinotis, namely the *western* (Chilian coast range).

*Note*—The existence of this ring-shaped continent *Mesozonia* in Upper Cretaceous times is extremely important for marine zoogeography. The distinction of two types of marine faunas, the MEDITERRANEAN and the PACIFIC, is well known among geologists, and this continent furnishes an explanation for this differentiation: all parts of the oceans lying to the *north* of Mesozonia—as far as the present knowledge goes—possess the *Mediterranean type*, all parts to the *south* of it exhibit the *Pacific type*.<sup>1</sup> In subsequent times both types of marine faunas frequently communicated, but there was never a complete fusion of both elements, and finally they developed into the *Atlantic* and *Indo-Pacific types* of the present marine fauna, the *Atlantic* being a continuation of the *Mediterranean*. In later Tertiary and recent times the differences of both were again emphasized, chiefly on account of the development of an ARCTIC and ANTARCTIC TYPE through the action of climatic agencies, which prevented their communication in the northern and southern regions of the earth. At present both original types which, as we have seen, go back to the Cretaceous, are restricted to the circumtropical belt, and are absolutely separated.

*c. Lower Tertiary.* (See Fig. 7, p. 383.)

The following changes appear:

The ring formed by *Mesozonia* was interrupted at three places: 1. between *Guiana* and *Africa*; 2. in *Central America* (Panama region); 3. between *Africa* and *Southeast Asia*. This latter inter-

<sup>1</sup> Of course, there are apparent exceptions. The Lower Senonian deposits of western Venezuela possess Mediterranean character (see Gerhardt, *N. Jahrb. Miner., etc.*, Berl., B. 11, 1897), but this is possibly explained by the assumption that they formed part of the Caribbean Sea just formed (see above, p. 343). The Mediterranean character of the Lower Cretaceous of Colombia, Ecuador and Peru is easily explained by the Orinoco strait.

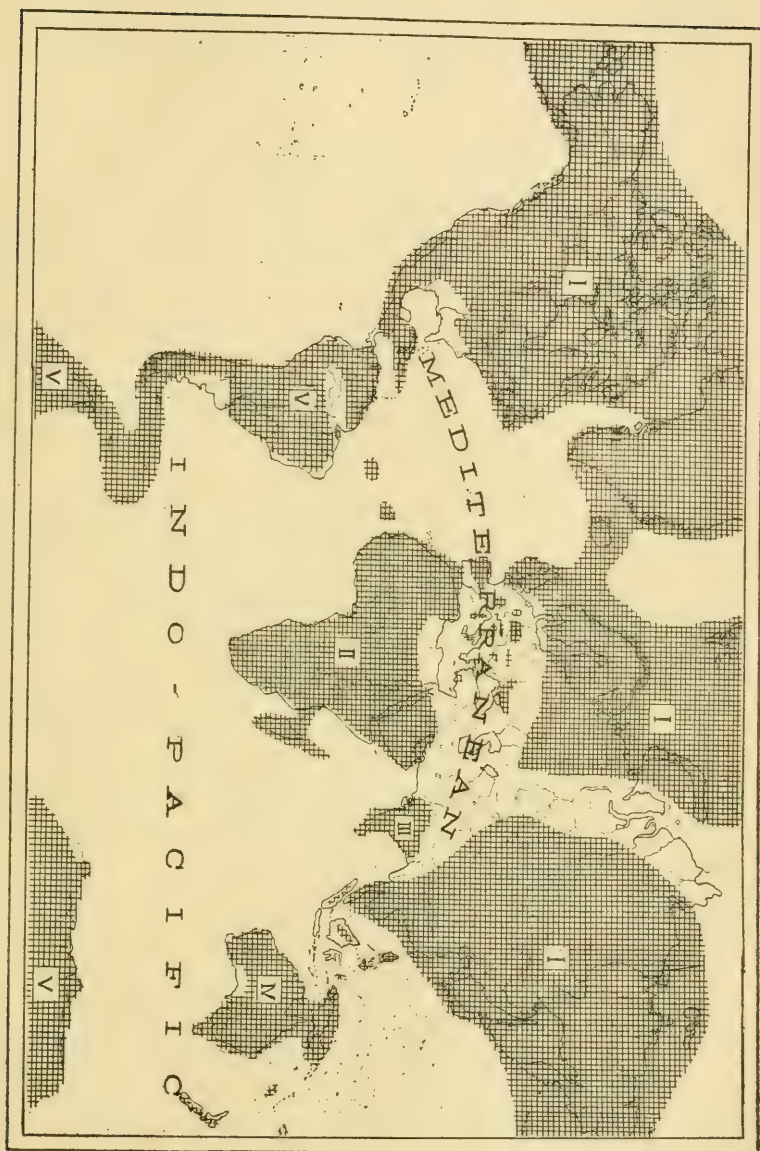


FIG. 7. Distribution of land and water during the *Lower Tertiary* period.

ruption is a double one, the Lemurian bridge between *Madagascar* and *India* being destroyed and *India* becoming again disconnected from the *Sinic land*.

The *southern part of Antillia* (with *Guiana*) becomes united with *Archiplata*.

*Archiplata* becomes connected with *Antarctica*.

*Antarctica* is cut off from *Australia*.

This results in the following five isolated continental masses:

I. *Sino-Nearctic continent*. Composed of the whole of *North America* (including possibly the *Scandinavian mass* in Europe), the northern parts of *Central America* and of *Eastern Asia* (*Sinic land*).

SINO-NEARCTICA comes very near to what von Ihering has called *Archiboreas*, with the exception that Europe does not belong to it. Von Ihering's *Archiboreas* is almost identical with the "*Holarctic region*," only from the latter the "*Sonoran region*" (southern North America) is excluded.

II. OLD TERTIARY AFRICA. This mass nearly approaches to present conditions, but still includes *Madagascar* and *Arabia*.

III. THE INDIAN ISLAND. A very small part, hardly worth the name of a continent, but here so-called in order to emphasize this important stage in the development of southern Asia.

IV. AUSTRALIA, which closely resembles its present form.

V. *Archinotis* and *Archiplata*, together with the *southern parts of old Antillia* (northern South America). This largely represents present *South America* with the addition of the *Antarctic land*. If we are to choose a name for it, we should like to propose NEONOTIS, in allusion to its relation to the older (Upper Cretaceous) *Archinotis* and the *Neotropical continent* of recent times.

d. *Upper Tertiary*. (See Fig. 8, p. 385.)

The following are the most important changes:

*Sino-Nearctica* is greatly enlarged, and becomes connected with the following parts: 1. in the Old World, with the island of *India*, with *Africa*, with the *European Archipelago*, and with *Scandinavia*; 2. the *Nearctic part of Sino-Nearctica* becomes connected, in the region of the Isthmus of Panama, with *Neonotis* (South America).

*Madagascar* is cut off from *Africa*.

*Antarctica* becomes separated from *South America*.



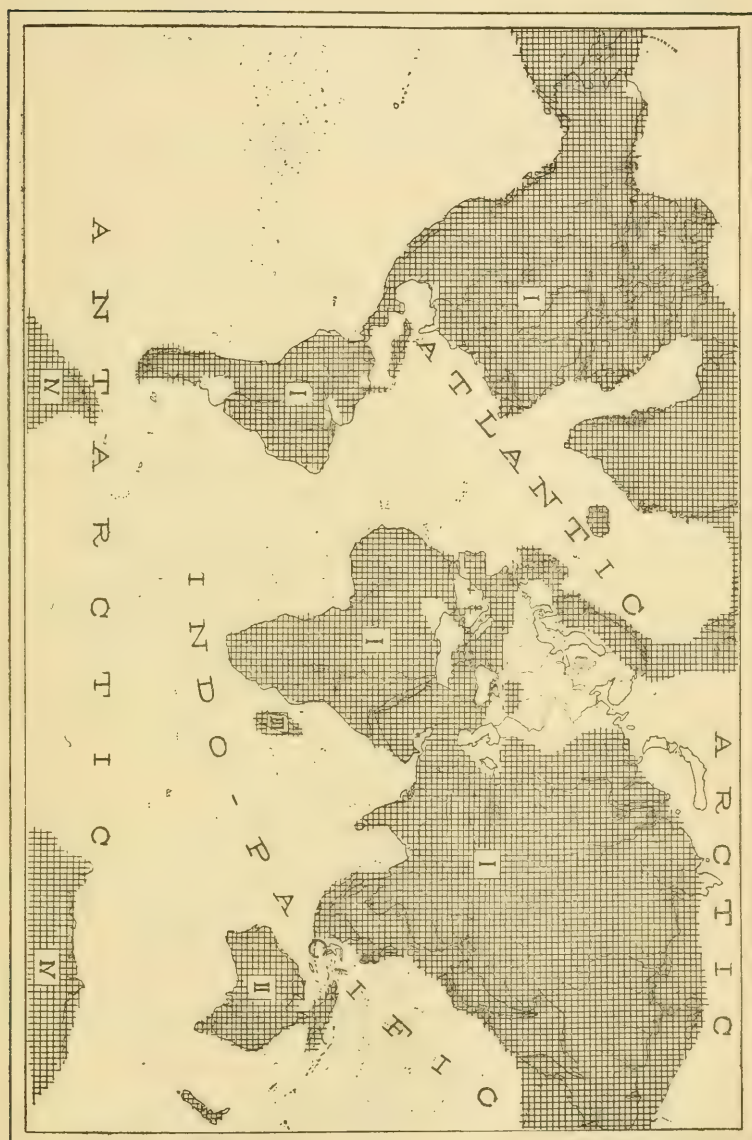


FIG. 8. Distribution of land and water during the *Upper Tertiary* period.

The result is :

I. *One large, continuous, continental mass*, comprising almost all of the *Old* and *New Worlds*. We may call it HOLOGÆA. It is composed, not only of the *Old World*, together with *North America* (*Arctogæa* of previous authors), but also of *South America* (*Neogæa* of previous authors).

Separated from it, we have only the following smaller parts of old continental masses :

II. AUSTRALIA, which may be regarded as a second continent.

III. MADAGASCAR, which is merely an island.

IV. ANTARCTICA, which, on account of the deterioration of the climate, loses its character as a centre for the origin of life.

*Note*—Here we have the *greatest continuity* of land masses of the earth that ever existed : practically all parts of the world that are important zoogeographical centres were mutually connected, with the exception of two comparatively small sections, Australia and Madagascar, and the barren regions of Antarctica.<sup>1</sup> This union of old centres of radiation had a very important result : we must attribute to it the fact that the distribution of many continental forms of life has been rendered confused, and the difficulty at the present time in tracing the origin of the different groups. Of course, Upper Cretaceous Mesozonia and other connections of Pre-Miocene times have had their share in effacing many of the original features of distribution, but *Late Tertiary Hologæa is the chief cause of uniformity in distribution* : in most cases "cosmopolitan" distribution, with the exception of Australia and Madagascar, may safely be referred to these Upper Tertiary conditions.

*e. Recent time.*

The most important changes that brought about the present distribution of the continents is the *separation of North America from Asia by Bering Strait, and of North America from Europe*. Thus we obtain a recent zoogeographic division into parts that represent important centres of distribution :

I. *Old World* (Europe, Asia, Africa). This agrees partly with Sclater's *Arctogæa*, except that North America is excluded. We may choose for it the name EUGÆA.

<sup>1</sup> I think that in Late Tertiary times Antarctica was not so desolate and destitute of life as it is now, but there is no doubt that the present character began to develop.

II. *New World* (America). This is *North America* and Sclater's *Neogæa*. I think there is no objection to use NEOGÆA for the whole of the "New World."

III. *Australia*. This is Sclater's NOTOGÆA.

IV. MADAGASCAR. Although of small size, the historical development warrants a consideration of Madagascar as a separate centre. In fact, it is—aside from Australia—the oldest isolated part of the world.

V. ANTARCTICA. This is no longer a centre of radiation; it is now barren of continental life.

*Note*—We claim that this division solves the problem of zoogeographical research as indicated by Osborn, and amended in the introduction (see p. 269, footnote 3): it unites historically and genetically past and present conditions of distribution of continental life—that is to say, it gives a division that is founded upon the present physical features of the earth's surface as related to life, and pays due attention to the past history of the earth. But this division takes into consideration only the chief *topographical* characters; yet there are others, especially those connected with *climatic* differentiation, which are apt to furnish additional points of view in dividing the earth in zoogeographical units. By using the latter we shall arrive, with only slight changes,<sup>1</sup> at *Wallace's regions*, which, as we have mentioned above (p. 271), are well supported by *physical characters*, although Wallace constructed them according to entirely different principles.

## B. HISTORY OF THE DISTRIBUTION OF CRAYFISHES.

(Compare Fig. 1, p. 275.)

1. In the *Lower Cretaceous* we are to assume that the ancestors of the *Potamobiidæ* and *Parastacidæ* lived in *Sino-Australia*, possibly extending to its southern extremity, Antarctica.

2. During the *Middle Cretaceous*, *Astacoides* reached Madagascar by way of the Lemurian land-bridge, coming from the Sinic continent. Shortly after this, in the *Upper Cretaceous*, the separation of eastern Asia and Australia took place, resulting in the differentiation of the families *Potamobiidæ* (in the Sinic continent) and *Parastacidæ* (in Archinotis). At the same time, the *Potamobiidæ* extended their range into *western North America*, going as far as *Central America*. Thus, in the *Upper Cretaceous*, the *Potamobiidæ*

<sup>1</sup> This refers to Madagascar.

extended over a great part of *Mesozonia*, from southeastern Asia over northwestern America to southern Mexico, and, in more primitive forms (approaching *Astacoides*), extending even from southern Asia across India to Madagascar.<sup>1</sup>

3. In *Lower Tertiary* times, the genus *Potamobius* gives origin, in *Mexico*, to the genus *Cambarus*, and this spreads over the *eastern parts of North America*. The *Parastacidae* of Archinotis extend from Chili to *northern Argentina* and *southern Brazil*, and the family is divided into an Australian group (which splits up in several genera) and a group belonging to Neonotis (*Parastacus*).

4. In *Upper Tertiary* times (and later), the *Potamobiidae* from eastern Asia reach *western Asia and Europe*, and the *Parastacidae* become restricted to Australia, New Zealand and South America.<sup>2</sup>

#### C. HISTORY OF THE DISTRIBUTION OF FRESHWATER CRABS.

(Compare Fig. 3, p. 297.)

1. In the *Upper Cretaceous*, freshwater crabs of the family *Potamonidae* existed in parts of *Mesozonia*, beginning in India (possibly going eastward to the Malaysian islands), and extending over the Lemurian bridge to Africa, Guiana and Central America.<sup>3</sup>

2. In the beginning of the *Lower Tertiary*, we find this area divided into two main portions. The one comprises *parts of America*: the northern parts of Neonotis and the southern parts of Sino-Nearctica (northern Central America), which are again separated from each other. These regions are inhabited by the subfamily *Potamocarcininæ*. The second main portion, occupied by the subfamily *Potamoninæ*, is formed by *Africa* and *India*, and this, during this time, is again divided into two sections, an *African* (including Madagascar) and an *Indian*.

3. In the *Upper Tertiary* (and later), the two sections of the range of the *Potamocarcininæ* become reunited, so that this subfamily now occupies the *West Indian region, Central America and northern South America*. Also the immigration in the *Lesser Antilles*

<sup>1</sup> The possible cause of the check to the farther distribution of the crayfishes over Mesozonia, westward beyond Madagascar and south- and eastward beyond Central America, will be discussed below (see p. 391).

<sup>2</sup> The Madagasian form, *Astacoides*, therefore does not belong to this stock, but should form a group by itself.

<sup>3</sup> It will be noticed that the distribution of crayfishes and crabs in Mesozonia is almost mutually exclusive: they came into contact only in Lemuria (and South Asia) and northern Central America. See below, p. 391.



occurred at this time. The *African* stock of the *Potamoninæ* remains practically unchanged, the *Madagassian* forms alone becoming separated from it; the *Indian* stock spreads over the *Malaysian islands* to *North Australia* and *Japan*,<sup>1</sup> and further, sends out a westward branch over *western Asia*, reaching *Southern Europe* and *Northern Africa*.

#### D. DISTRIBUTION OF *ÆGLEA* AND THE TRICHODACTYLINÆ.

(Compare Fig. 2, p. 296, and Fig. 4, p. 311.)

1. The remarkable resemblance of the range of *Æglea* to that of *Parastacus* suggests identity of origin. This would mean that *Æglea*, in the *beginning of the Tertiary*, inhabited *Chili*, and migrated, at this time, into *northern Argentina* and *southern Brazil*. Since there are no closer relations to this peculiar genus in any other part of the world, *Æglea* apparently is indigenous to *Chili*, *i.e.*, to the northern extremity of the American part of *Archinotis*, and subsequently extended only into the southern part of *Archiplata*. Of course, the opposite direction of migration also is possible.

2. As we have seen above (p. 312) the distribution of the *Trichodactylinæ* offers no remarkable feature. It belongs to the Atlantic slope of present South America (the *Neotropical region* of Wallace) and seems to have formed under the *recent conditions*. Possibly, this subfamily is a new addition to the freshwater fauna, and immigrated from the marine littoral of the Atlantic. Further investigation of this question, together with a closer study of the morphology and systematic relations of this group are very desirable.<sup>2</sup>

#### PART III. CLIMATIC AND BIOGEOENOTIC<sup>3</sup> BARRIERS TO THE DISTRIBUTION OF CRAYFISHES AND CRABS.

In the foregoing discussions we have repeatedly called attention to some distributional facts which we were unable to explain. For

<sup>1</sup> This extension began possibly as early as the Upper Cretaceous and Lower Tertiary.

<sup>2</sup> Everything here depends on the systematic position and affinity of this group. If it should be a primitive one, and really belong to the *Potamonidæ*, it is possible that it reached Brazil in *Lower Cretaceous* times, when it formed part of *Archhelenis*. Its isolation in *Upper Cretaceous* *Archiplata*, which was not fully destroyed when it became a part of *Lower Tertiary* *Neonotis*, would explain its isolated morphological position. In the Tertiary this subfamily would then have extended its range northward.

<sup>3</sup> As to the term "Biogeoenotic barrier," compare Ortmann, *Grundzuge der marinen Tiergeographie*, 1896, pp. 41 and 70.

convenient study we may put them together here under the following heads:

1. Explanation of the absence of *Potamocarcininae* in Brazil south of the Amazonas river.
2. Explanation of the absence of *Parastacidae* in Middle and Northern South America.
3. Explanation of the absence of *Astacoides*-like forms in Africa.
4. Explanation of the absence of *Potamobiidae* in Central and South America.
5. Explanation of the absence of crayfishes in Central and South Asia and on the Malaysian islands.

We can dispose of the first point with ease; indeed, we have indicated above the chief cause of it. The *Potamocarcininae* originally (in the Upper Cretaceous) occupied only the region to the north of the Amazonian interoceanic connection. In the Tertiary we have a connection of northern South America with the Brazilian mass (Archiplata) in the west (region of the Cordilleras), and we see that the crabs availed themselves of this opportunity and spread over the mountainous regions of Ecuador, Peru and Bolivia, possibly here reaching a climatic southern boundary. The Amazonas valley, however, remained sea during a much longer time and was gradually and slowly filled by the deposits carried down from the mountains. Thus, up to a comparatively recent time, it was impossible for the *Potamocarcininae* to cross this depression. That there now exists a possibility of crossing this old barrier is shown by the existence of at least one species on the southern banks of the mouth of the Amazonas near Pará.

In regard to the second point—the absence of *Parastacidae* in the main (tropical) part of Brazil—I can offer no explanation. They must have immigrated into Southern Brazil early in Tertiary times, and possibly we have to deal here with a climatic barrier.

We may take together the other three points, since they apparently are subject to identical causes. Looking at the original distribution of the crayfishes and crabs in Upper Cretaceous times, we have to note the very remarkable fact (see p. 388, footnotes 1 and 3) that both together occupied the whole of Mesozonia, but each different parts of it almost to their mutual exclusion. The crayfishes seem to have existed in the Asiatic part of this conti-

mental ring and in the North American as far as the northern section of Central America. There they gave place to the freshwater crabs, which extended thence to Northern South America, Africa and Lemuria, where they came again into touch with the crayfishes.

The same fact, namely, that crayfishes and crabs are mutually exclusive, holds good for their distribution in recent times. This fact was first pointed out by Milne-Edwards; it has also been mentioned by Faxon, and the present writer<sup>1</sup> has used it for the explanation of some of the features in their distribution. It seems, therefore, that the crabs are more vigorous and active than the crayfishes, and that wherever they came into actual contact the latter were exterminated by the former. It is true there are some countries from which both types of Decapods have been reported, namely, Mexico, Northeastern Australia and Madagascar; but we have no report that both are found associated in the same localities and in the same rivers, streams, ponds or lakes, and it is very likely that just in these regions crabs and crayfishes inhabit stations of a different character. The closer investigation of these conditions would be most interesting.

If we apply this idea, that the presence of crabs forms a biocoenotic barrier to the crayfishes in the former distribution of both, we obtain the following result:

The crayfishes are geologically older than the crabs. They existed, in Lower Cretaceous times, in Sino-Australia, and consequently also in the region of Southeastern Asia and the Malaysian islands. In the Middle Cretaceous they sent a branch (*Astacoides*) across India to Madagascar. But in the Upper Cretaceous the freshwater crabs arrived (or originated) in the same region (Lemuria) and extended into Southern Asia and the Malaysian Archipelago, everywhere exterminating the crayfishes, namely, in India, Southeastern Asia (Farther India and China) and on the islands. They not only acted as a check to the distribution of the crayfishes, but directly annihilated them. Only in Madagascar *Astacoides* survived, probably because in this island it inhabits parts that have not been occupied by the crabs.<sup>2</sup> On the other hand,

<sup>1</sup> See Ortmann, in *Zool. Jahrb. Syst.*, Vol. 9, 1896, p. 593 f., and in Bronn's *Klassen und Ordnungen*, Vol. 5, 1901, p. 1289.

<sup>2</sup> Possibly the large size of *Astacoides* has something to do with its survival. *Astacoides* is—aside from some South Australian species—by far the largest type of all crayfishes.

the original presence of crabs in Africa at about the middle of the Cretaceous would explain the fact that no crayfishes are found on this continent; but, on the other hand, there is the possibility that crayfishes once existed there, but have become extinct on account of the increase of crabs in this country.

Then, again, after the crayfishes had, in Upper Cretaceous times, occupied western North America and Mexico, they met here with the crabs which came from the south, and their farther advance was checked by this biocoenotic barrier.

The question remains, why did the crabs not advance beyond their present (and old) boundaries in China, Australia and Mexico? If it is correct that the existence of crabs forms a barrier to the extension of the crayfishes, the opposite cannot be the case. The presence of crayfishes would not put a stop to a farther dispersal of crabs. But here, I think, we have to deal with climatic barriers. All freshwater crabs are truly tropical animals, entering in only a few cases subtropical countries, but never temperate or cold regions, and thus it seems that the northern boundaries of the *Potamonide* in China and Mexico and the southern in Australia are due to the climate of these respective parts. The same seems to be true in Europe, Western Asia and in Bolivia, where the northern, resp. southern boundaries are apparently given, in a large part, by some features of the climate.

It will be noticed that in applying this principle to the past distribution of the crabs it is necessary to assume the existence, in earlier Tertiary and even Pretertiary times, of climatic differences *on the continents*, although we do not believe in a climatic differentiation of the oceans of the Mesozoic period. But this is entirely in keeping with our opinion expressed in a previous paper.<sup>1</sup> And, further, I do not mean to say that the present climatic boundaries of the crabs are identical to those of former times. On the contrary, it is quite possible, for instance, that in China the crabs formerly extended farther north, and in Europe we know positively that the European species did so in Diluvial times, reaching as far as Hungary, where it does not now live (see above, p. 376, footnote). The southern boundary of the crabs in Australia, however, seems to be original and has not retreated equatorward, since these

<sup>1</sup> Ortmann, A. E., "An Examination . . . of Climatic Zones in Jurassic Times," in *Amer. Journ. Sci.*, Vol. 1, 1896, p. 270, footnote.



crabs arrived there presumably in a very recent period. Only the boundary in Mexico needs investigation, but possibly here it is not temperature that puts a stop to the northern advance of the crabs, but another climatic factor, namely, the arid or semiarid character of the country lying to the north of the actual boundary, which possibly has existed from the beginning of the Tertiary.

The above considerations would sufficiently explain the third, fourth and partly the fifth points (see p. 390), namely, the absence of crayfishes in Africa, the absence of *Potamobiidæ* in Central and South America and their absence in South and Southeast Asia and on the Malaysian islands. They could not enter Africa and could not go beyond Mexico on account of the presence of crabs in these parts, and in Southeastern Asia and Malaysia they must have once existed, but have succumbed under the onslaught of the crabs. This latter cause seems also to control the distribution of the crabs and crayfishes in Southern Europe (see p. 377). It does not explain, however, the absence of crayfishes in Central Asia, and, as regards this point, we are unable to offer any reasonable explanation (see p. 378 and footnote).

#### CONCLUSION.

Although we have tried to advance explanations for many of the puzzling facts in the distribution of the freshwater Decapods discussed here, we are to bear in mind that the ideas brought forward are largely hypothetical and tentative. In many respects we have found a wonderful agreement between the distributional facts and what is known about the geology and tectonics of the respective parts, and it was one of my chief purposes to point out that it *is* possible to more closely correlate zoogeography and geology. But, nevertheless, I am fully aware of the danger that lies in our incomplete knowledge, not only of the geological configuration of the different countries here discussed, but also in the deficiency of the chorological facts at hand.

I wish most strongly to emphasize that I do not believe in all cases to have correctly revealed the ancient relations of land and water, and I think that my ideas of the old continents need confirmation and probably modification. I have only tried to give a representation of what I think of the changes that have taken place during the earth's history, as far as the present state of our knowledge permits of any conclusions in this respect, and I earnestly

wish that my opinions may be investigated by other authors and compared with material furnished by other groups of animals, as well as with more complete and reliable geological observations to be made in future. The way in which such investigations should be carried on has been indicated in this paper.

Finally, I want to point out that most of the ancient continental connections here discussed are not treated for the first time, but have been hinted at or more or less closely investigated by previous authors, zoogeographers as well as geologists. But, unfortunately, the former have not generally paid much attention to the results obtained by the latter, and *vice versa*. Just this lack of a broader view, chiefly among zoogeographers, has induced me to attempt to harmonize both sets of facts, and the results here presented are possibly apt to serve as an apology for having undertaken this task although much preliminary work remains to be done.

#### APPENDIX.

##### RELATION OF THE MARINE DECAPOD FAUNAS OF THE EASTERN AND WESTERN SIDES OF TROPICAL AMERICA.

We have mentioned above (p. 359, footnote) that the facts furnished by the characters of the marine faunas of either side of Central America are frequently misunderstood or misrepresented. In order to get at a proper understanding of the relations of the Atlantic and Pacific Oceans, as revealed by these facts, I shall endeavor here to give a (incomplete) list of identical, resp. closely allied forms of Decapod Crustaceans, which are especially apt to throw a light on this question.

I have made it a point to include in this list only such forms as give plain and unmistakable indications in this respect, that is I have used only those cases in which the relations between the Panamic and Caribbean region are the closest known, which, generally, is self-evident only when the respective forms (mostly species of the same genus) are not known outside of American waters. In genera or groups, where representatives are also known from other parts (especially the Indo-Pacific region), it is not always easy to determine the relation of the different forms, and the question whether the West and East American forms are the most closely allied ones remains unsettled: therefore I shall disregard such instances.

Nevertheless, I am able to offer here a list that is quite large.<sup>1</sup>

PACIFIC SIDE.	ATLANTIC SIDE.	REMARKS.
<i>Panulirus interruptus</i> (Rand.).	<i>P. argus</i> (Latr.).	The Californian species is <i>the</i> most closely allied form, although the genus is circumtropical.
CALCINUS TIBICEN (Hbst.), Ecuador (Nobili, <i>Boll. Mus. Torino</i> , Vol. 16, 1901, p. 26).	C. TIBICEN (Hbst.).	
PETROLISTHES GALATHINUS (Bosc.).	<i>P. GALATHINUS</i> (Bosc.).	We exclude <i>P. armatus</i> Gibb. as a circumtropical species.
PACHYCHELES PANAMENSIS Fax. (see Nobili, <i>l. c.</i> , p. 19).	<i>P. PANAMENSIS</i> Fax.	
Genus <i>Lepidopa</i> .	Genus <i>Lepidopa</i> .	Number of species doubtful, but exclusively found in the West Indies and Low. California. The species on both sides different.
<i>Remipes strigillatus</i> Stps.	<i>R. cubensis</i> Sauss.	Also in West Africa. This group of the genus is found nowhere else. The genus is circumtropical.
<i>Albunea lucasia</i> (Sauss.).	<i>A. gibbesi</i> and <i>pareti</i> .	No other species of the genus are so closely allied, although the genus is circumtropical.
HIPPA EMERITA (L.).	H. EMERITA (L.).	Genus circumtropical.
<i>Hypoconcha panamensis</i> Sm.	<i>H. sabulosa</i> (Hbst.). <i>H. arcuata</i> Stps.	Genus found nowhere else.
ETHUSA AMERICANA A. M.-E.	E. AMERICANA.	Genus cosmopolitan.

<sup>1</sup> Where no references are given, the facts are taken from Ortmann, in Bronn's *Klass. u. Ordn.*, Vol. 5, 1900, p. 1275, and from my unpublished revision of the respective groups for the "Thierreich."

Identical species are printed in SMALL CAPITALS; the most important forms, where the genus is not found outside of American waters, are printed in *italics*.

PACIFIC SIDE.	ATLANTIC SIDE.	REMARKS.
<i>Ranilia angustata</i> Stps.	<i>R. muricata</i> M.-E.	<i>Ranilia</i> M.-E. includes <i>Notopus</i> d. H. and <i>Raninops</i> A. M.-E. The species mentioned here form a natural group, which is not found elsewhere.
<i>R. fornicata</i> (Fax.).	<i>R. stimpsoni</i> (A. M.-E.). <i>R. constricta</i> (A. M.-E.).	
<i>Lithadia cumingi</i> Bell. <i>L. digueti</i> Bouv.	<i>L. cariosa</i> Stps. <i>L. miersi</i> Ortm. <i>L. cadaverosa</i> Stps. <i>L. cubensis</i> Mrts. <i>L. pontifera</i> Stps.	This genus is found nowhere else.
<i>Uhlias ellipticus</i> Stps.	<i>U. limbatus</i> Stps.	Genus found nowhere else.
<i>Persephona subovata</i> (Rthb.). <i>P. orbicularis</i> Bell. <i>P. edwardsi</i> Bell. (= ? townsendi (Rthb.)).	<i>P. punctata</i> (L.).	Of one species ( <i>P. lichtensteini</i> Leach) the habitat is unknown, but it is certainly from America. The genus is not found elsewhere.
<i>Hepatus chilensis</i> M.-E.	<i>H. epheliticus</i> (L.). <i>H. annularis</i> (Ol.).	Several doubtful species, but none outside of American waters.
<i>Hepatella actua</i> (Stps.). <i>H. laevis</i> (Rthb.). <i>H. lata</i> (Fax.). <i>H. amica</i> Sm.	<i>H. tuberosa</i> (Stps.).	<i>Hepatella</i> = <i>Osachila</i> . One species, <i>H. stimpsoni</i> (Stud.), at Ascension Island. No other species from any other part of the world.

The following are taken from Rathbun, *U. S. Nat. Mus.*, Vol. 15, 1892:

<i>Pericera triangulata</i> Rthb. <i>P. contigua</i> Rthb.	<i>P. cornuta</i> (Hbst.). <i>P. atlantica</i> Rthb.	Genus found nowhere outside of America.
<i>Othonia nicholsi</i> Rthb.	<i>Othonia</i> (4 species).	Genus not found outside of America.
<i>Mithrax</i> (4 species).	<i>Mithrax</i> (14 species).	Genus not found outside of America.



The following are taken from Rathbun, *U. S. Nat. Mus.*, Vol. 16, 1893:

PACIFIC SIDE.	ATLANTIC SIDE.	REMARKS.
<i>Libinia macdonaldi</i> Rthb.	<i>L. spinimana</i> Rthb.	Other species known from both sides, and possibly from other parts of the world, but these two are especially closely allied.
<i>Pelia</i> (2 species).	<i>Pelia</i> (2 species).	Genus found nowhere else.
EPIALTUS BITUBERCULATUS.	E. BITUBERCULATUS.	There are four other species on the Pacific side. The genus is found nowhere else.

The following is taken from Rathbun, *ibid.*, Vol. 18, 1896, and *Proc. Biol. Soc. Wash.*, Vol. 10, 1897:

<i>Callinectes</i> (4 species).	<i>Callinectes</i> (6 species).	All Pacific species different from the Atlantic. Three of the Atlantic species also found in West Africa. Genus not found elsewhere.
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The following is taken from Nobili, *Boll. Mus. Torino*, Vol. 16, 1901, p. 32:

CRONIUS RUBER (Lmck.)	C. RUBER.	This species also in West Africa, but nowhere else.
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In this list we see there are *seven identical species*. The rest are more or less closely allied, but the affinity is always so close that it is not equaled in any other part of the world, with the exception of West Africa, where some of the types have been found that are common to the east and west sides of America, but are lacking everywhere else. This affinity of the West African littoral fauna is a well-known fact, and there is nothing remarkable about it, since a communication between both sides of the Atlantic is possible in many cases even at present times.

Aside from this, a close relation of the western and eastern faunas of the Central American shores is revealed at a glance.<sup>1</sup> Hill says (*l. c.*, p. 267) that the recent faunas of the opposite sides of the isthmus are so distinct that the communication of waters must have belonged to a very remote time, and that there has been probably no communication since Miocene. We may modify this a little and say that the affinities of the Decapod fauna of the Atlantic and Pacific are unmistakable, and *that we have ample and convincing evidence that there must have once been a connection.* The scarcity of identical forms (which in part are not beyond doubt), and the demonstrated fact that generally one (or more) species of the respective genera replace each other on either side of America, being distinctly different, although closely allied, shows conclusively that this connection cannot have been of a very recent date. I think that the Decapods confirm Hill's opinion that *there was no communication whatever of both oceans since Miocene time*, and we may add that probably the similarity of both faunas is to be referred in most cases to the Eocene and Oligocene interoceanic connection across the isthmus. After this had been closed sufficient time has elapsed to generally change the characters of the once identical Pacific and Atlantic stock and to render them different species, while only a few have preserved their original characters and are to be regarded as identical species.

Of course it is possible that some of the similarities of the Pacific and Atlantic faunas go back to earlier (Mesozoic) times, when the

<sup>1</sup> In speaking of a close resemblance of these faunas, I wish to avoid being misunderstood. There are cases that show a close resemblance, but this does not mean that both faunas are closely related in *all* respects; on the contrary, there are other elements on both sides of Central America that are peculiar to only one of them. The Panamic fauna, for instance, contains Indo-Pacific elements and a very peculiar element that belongs to the whole western coast of America (from the Western United States to Chili). I have called attention to this element in a former paper (*Zool. Jahrb. Syst.*, Vol. 9, 1896, p. 582 ff.), but I have been entirely misunderstood by von Ihering, who says (*Rev. Mus. Paulista*, Vol. 2, 1897, p. 379) that my theory of a migration along this coast is disproved by the fact that different faunas succeed each other along this coast from the south to the north. This is quite true, but it does not disprove my theory, since I never meant to say that the whole of the West American fauna has reached these parts by migration from north to south or *vice versa*. On the contrary, only a part of it belongs to this category, and there are other components of the West American fauna which came from quite different sources.

Mexican, Orinoco and Amazonas interoceanic connections existed. But this would not influence our general result that the communication of the oceans was interrupted definitively in the Miocene.

We have, beginning in Mesozoic times, a differentiation of two types of marine faunas, a Mediterranean and a Pacific, but these faunas communicated with each other at certain points and were completely separated for a comparatively short period in the Upper Cretaceous by the continent of Mesozonia (if this separation was at all complete at any time).<sup>1</sup> Generally the Mediterranean fauna belongs originally to the northern hemisphere, the Pacific to the southern, except that the latter largely encroached upon the former in the region of the Northern Pacific. This arrangement was completely upset during the Tertiary, so that at present the Atlantic fauna (containing chiefly the descendants of the old Mediterranean types) and the Pacific fauna are divided, not by a line running east and west, but by two lines running generally north and south (in America and in the Old World). Besides, the Arctic and Antarctic types have been added, the former being an offshoot of the Mediterranean, the latter of the Pacific type.<sup>2</sup>

While in former times, in the Mesozoic and Lower Tertiary, a decided tendency prevailed to mix the marine faunas of the world and make them more or less uniform, which tendency was checked only temporarily, we have, from the Miocene upward, a complete separation of two marine types of fauna,<sup>3</sup> which, however, still possess certain features in common that are due to conditions prevailing in earlier times, and with respect to Central America these conditions (interoceanic connections) were present for the last time in the Older Tertiary (Eocene and Oligocene).

<sup>1</sup> We possess evidence that Mesozonia was interrupted for shorter periods within the Upper Cretaceous, for instance, in the region of British Colombia (see Koss-mat) and in Western Venezuela (see above, p. 343).

<sup>2</sup> In opposition to the belief of some authors (Pfeffer, Murray) that both Polar faunas are strikingly similar, I have always held the opinion (see review of the literature in *Americ. Natural.*, Vol. 35, 1901, p. 139 ff.) that this is not so. We see here also that the origin of these faunas is different, the one being derived from the old Mediterranean, the other from the old Pacific fauna, the differences of which, although obscured during the earth's history by frequent interchanges, go back to Mesozoic times.

<sup>3</sup> The complete separation was brought about not only by topographical factors, but chiefly by the additional action of climatic differentiation. See Ortmann, *Grundzüge der marin. Tiergeograph.*, 1896, p. 40.

It is a very remarkable fact that the interoceanic connection of the Mediterranean and Pacific type of marine faunas, existing in Western and Southern Asia (Tethys and Strait of Bengal), was ended at about the same time, in the Miocene, by the elevation of Western Asia and its union with Africa and Europe.

PRINCETON UNIVERSITY.





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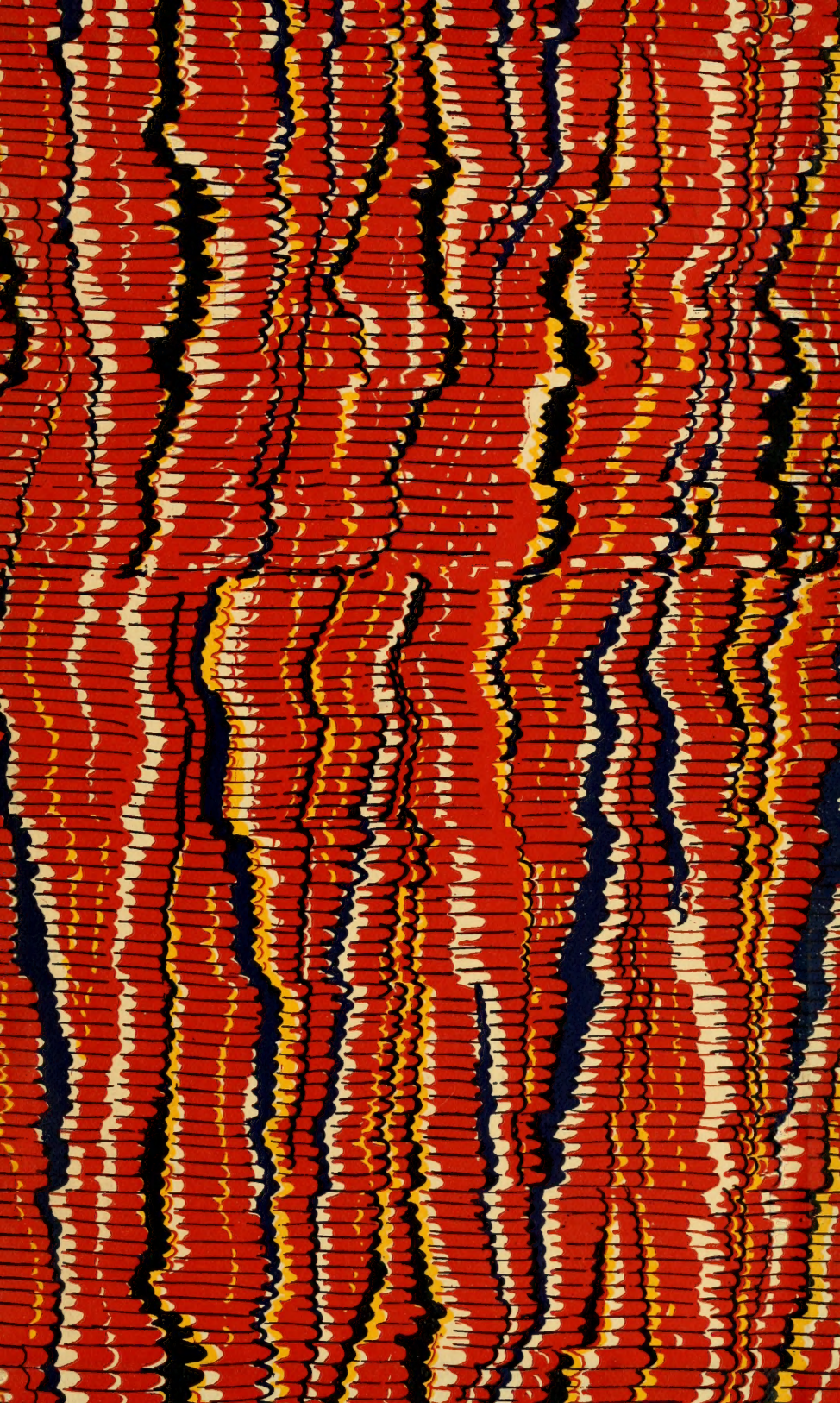














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